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EUROPEAN FLORISTIC AND TAXONOMIC STUDIES

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CONFERENCE REPORT

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Edited by
S. M. WALTERS
with the assistance of
C. J. KING

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EUROPEAN FLORISTIC AND TAXONOMIC STUDIES

B.S.B.I. Conference Report No. 15

A Conference held in Cambridge

29 June to 2 July 1974

Edited by S. M. WALTERS

with the assistance of C. J. KING

Published for

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PREFACE

The content of this Preface needs a little explanation. Normally in a Conference Report the reader might expect a separate Editor's Preface and an Introduction, but on this occasion such a division seemed unwieldy, because both these contributions were expected from the pen of the same author! I hope, therefore, that I may be excused for conflating Preface and Presidential Introduction into a single block of prose.

When the Botanical Society of the British Isles did me the honour of electing me President in 1973, I began to discuss with colleagues the possibility of holding a European Conference in Cambridge for the following year. There were several reasons why such a Conference seemed particularly appropriate. The first was that I had just been appointed to succeed John Gilmour as Director of the University Botanic Garden after his retirement on 30 September 1973, and such a Conference, using the facilities of the Botany School and the Botanic Garden, seemed to be a suitable inaugural activity for my first year. The second reason was that I had been much impressed by the joint Conference of the Society and the Royal Horticultural Society in 1972, the success of which owed much to the zeal and enthusiasm of my predecessor David McClintock; I asked myself what would be the most appropriate contribution which I might make to the series of Conferences held approximately biennially in recent years, and decided that the theme, then much under public discussion, of Britain as a part of the European Continent would be particularly appropriate. In 1973, the role of British taxonomic botany in Europe as a whole was very much in my mind because of my work as a member of the Editorial Committee of *Flora Europaea*; we were all much exercised by the problem of financing the final stages of this co-operative European project, and were heartened by the evidence of real practical support from colleagues in many European countries.

So the idea of the Society running a European Conference took shape, but an obvious difficulty remained. The Botanical Society of the British Isles has no paid officials, and even though the Honorary Secretary and all the other officers perform marvels of courteous efficiency in admin-

istering the Society's increasingly ambitious affairs, the burden of organizing a full-scale residential conference out of London could not and should not fall on the already overworked officers. I therefore early in 1973 approached Mrs Gigi Crompton, a Cambridgeshire botanist from whom amateur and professional alike in Cambridge have in recent years come to expect much devoted and efficient service, with the question – would she act as Honorary Conference Organizer? I felt that, if Mrs Crompton were prepared to act, I also could see my way to undertake the planning and preparation required; when she agreed, we were all set to begin the invitations, the bookings, the applications for financial help, and the many other chores which needed attention, if B.S.B.I. members and invited foreign guests alike were to be satisfied.

One other happy conjunction presented itself early in the planning. Several of our distinguished Honorary Members, including most appropriately John Gilmour himself, were achieving, or had already achieved, that 'Valhalla' state of 50 years' Membership, and the Council of the Society agreed to honour seven such members by an invitation to the Conference Dinner in King's College. In the event, two only were able to be present, but the Latin Oration in their honour delivered by the University Orator, Mr Patrick Wilkinson, to a text supplied in English by Mr John Raven (both Fellows of the College) added a special lustre to the proceedings.

On the Sunday, after the formal sessions at which the main papers were presented, a picnic lunch was served in the Research and Experimental Area of the Botanic Garden. The weather was kind, and the occasion took on a Continental flavour almost of a French *déjeuner* – an illusion which was certainly helped by the bottles of wine unexpectedly available. In the afternoon the demonstrations were inspected in the Laboratory, and after tea Dr Yeo and I showed the participants round the Garden, concentrating in particular on the Conservation role which we hope to develop in the next few years. After dinner, Dr Perring regaled a relaxed and sympathetic audience with a light-hearted illustrated talk on some of the 'Consequences of Mapping the Flora of Europe'.

Much more could be recorded of those peripheral events which did much to make the Conference such a pleasant experience. My own selection is perhaps a peculiar one, in that I was behind the scenes at various times, and formally presiding at others. I certainly derived great satisfaction from the obvious success of the Conference in providing, as we had hoped, an opportunity for our European guests to meet and get to know our own members, both 'professionally', as it were, in the sessions of the Conference itself, and more light-heartedly on the field excursions, at the reception in the Fitzwilliam Museum, or in the

much-appreciated bar of King's College. It was a particular pleasure to find that, in addition to our guest speakers, several foreign members of the Society came specially for the Conference, and that our own internal membership was excellently represented by a very satisfactory mixture of amateur and professional, young and old. Several of our foreign guests expressed admiration, astonishment, and even envy, at the vitality and range of our Society – a reminder that, in the amateur tradition of field botany in Britain, we have a most valuable asset most other countries lack. In all we had about 140 participants at the Conference, including 16 guest speakers from 11 different European countries.

In editing the material of the Conference for this publication, Mr Clive King and I have taken certain liberties, which should be briefly explained. Firstly, we have slightly altered the title, introducing the word 'taxonomic', so that the general reader would be prepared for the range of subject-matter covered by the papers. The order of the papers has been retained more or less as presented, beginning with the two general papers, one by Dr Stearn on the British contribution to European floristic studies, and the other by Dr Greuter on the history of floristic studies in Greece (where the contribution of foreign botanical work is, of course, particularly important), and proceeding to the particular taxonomic studies of familiar European genera. In these more specialist invited papers, we have permitted, or even encouraged, some re-drafting in the interests of clarity, but have tried to retain the particular flavour of the papers as delivered to the Conference. One of the conditions imposed on, and willingly accepted by, the invited speakers was that they should give their paper in English; it was, I know, a matter of considerable admiration on the part of many B.S.B.I. members to find how many of their European colleagues could satisfy this requirement with some distinction.

I must confess to a single area of disappointment – namely that, in spite of all our efforts, four of our invited foreign speakers were unable to get permission to attend. I had hoped that the general spread of the philosophy of *détente* in Europe would have made our task easier; it did not, alas, prove to be so, and the entirely free movement of people and ideas, even in such a 'neutral' science as ours, is still a dream for the future.

It remains for me to now record my personal thanks, and the appreciation of the Society, to a number of organizations and individuals with whose help we were able to run such a successful Conference. In the first place, we would wish to thank the Royal Society for a generous grant towards the fares, and the British Council for subsistence and (in some cases) travel grants, for our invited foreign speakers.

In addition, we gratefully acknowledge a grant for entertainment received from the University of Cambridge, and permission from Professor Percy Brian, who welcomed guests and participants at the opening session, to use the facilities of the Botany School and the Botanic Garden during the whole Conference. Thanks are also due to the Director of the Fitzwilliam Museum, Professor Michael Jaffé, and members of his staff, who arranged with us the excellent evening reception to see the remarkable exhibition of flower drawings from the Broughton Collection. The two field excursions which followed the main meetings were greatly appreciated, in spite of 'Atlantic' weather appropriate to the vegetation types visited, and our special thanks must be recorded to our members, Mr R. P. Libbey, Mr P. D. Sell and Mr E. L. Swann, leaders of the Norfolk field trip, and to Dr F. H. Perring and Mr M. Schofield (Monks Wood Experimental Station), and Mr G. Mason (Woodwalton Fen Nature Reserve) for the second day. A special word of thanks should also be recorded to Mr John Raven, who helped in three quite separate capacities, firstly in preparing the Latin Oration, secondly with botanical queries arising from the selection of the Broughton Collection drawings, and lastly in kindly receiving at his beautiful house, Docwra's Manor, Shepreth, a small but highly appreciative party of foreign guest botanists and their hosts on an extra excursion at the end of the Conference. Last, but by no means least, I must record my appreciation of the excellent work of the staff of my own College, King's, which housed and fed the Conference. It was very pleasant, after the event, to receive so many words of thanks particularly for the catering arrangements.

I have already expressed my total indebtedness to our excellent Conference Organizer, Mrs Gigi Crompton. To help her in the complex hour-by-hour detailed running of the Conference she had many willing colleagues, four of whom deserve particular mention – Mrs Mary Briggs, Mr and Mrs John Dony and Mr J. C. Faulkner. To these and all the 'B.S.B.I. team' I can only say, in tribute, that the President was left with no worries and no unexpected duties and therefore, to his great relief, found he had time to relax and enjoy the whole occasion!

A final, and special word of thanks is due to my assistant editor, Clive King, whose skill and patient attention to detail are revealed in this end-product of many hours' work.

S. M. WALTERS

CONFERENCE PROGRAMME

*Held at King's College, the Botany School, and the
Botanic Garden, University of Cambridge.*

Saturday, 29 June

OPENING SESSION

Chairman: Professor P. W. Brian, F.R.S., Professor of Botany, University of Cambridge

11.15–11.20 PRESIDENT'S OPENING REMARKS

Dr S. M. Walters

11.20–12.20 HISTORY OF BRITISH CONTRIBUTION TO EUROPEAN STUDIES

Dr W. T. Stearn

12.20–13.00 FLORISTIC STUDIES IN GREECE

Dr W. Greuter

13.15–14.15 Lunch, King's College

STUDIES IN COMMON EUROPEAN GENERA

Chairman: Professor C. D. Cook, Professor of Botany, University of Zürich

14.30–15.10 APOMIXIS IN A STERILE HYBRID SPECIES OF *POTENTILLA*

Dr R. Czapik

15.10–15.50 THE *VERONICA HEDERIFOLIA* GROUP

Dr M. Fischer

15.50–16.20 Tea

Chairman: Professor D. H. Valentine, Professor of Botany, University of Manchester

16.20–17.00 CARYOSYSTEMATIC STUDY OF SOME SPECIES OF THE GENUS
CENTAUREA

Dr C. Gardou

17.00–17.40 ASPECTS OF *CROCUS TAXONOMY*

Mr B. Mathew and Miss C. Brighton

17.40–18.20 STUDIES IN THE GENUS *MYOSOTIS*

Professor Dr J. Grau

19.30 CONFERENCE DINNER, King's College, in honour of the Honorary Members of the Society of 50 years Membership standing

Sunday, 30 June

CYTOTAXONOMIC AND HYBRIDIZATION STUDIES

Chairman: Professor D. H. Valentine

09.30–10.10 HYBRIDIZATION IN YELLOW-FLOWERED EUROPEAN *RORIPPA* SPECIES

Dr B. Jonsell

10.10–10.50 WILD HYBRIDS IN THE BRITISH FLORA

Dr C. Stace

10.50–11.20 Coffee

11.20–12.00 TAXONOMIC PROBLEMS IN THE FERN GENUS *POLYSTICHUM* CAUSED BY INTERSPECIFIC GENE EXCHANGE

Dr G. Vida

12.00–12.40 CYTOTAXONOMY OF THE GENUS *LEUCANTHEMUM* IN YUGOSLAVIA

Dr D. Papeš

13.00–14.00 Buffet lunch, Botanic Garden

14.00–16.00 DEMONSTRATIONS IN THE BOTANIC GARDEN LABORATORY

Opening remarks by Mr J. S. L. Gilmour, Cambridge

16.00–16.30 Tea

16.30–18.00 THE ROLE OF BOTANIC GARDENS IN CONSERVATION AND TAXONOMIC RESEARCH

Dr S. M. Walters: PERAMBULATION of the Botanic Garden

19.30 Dinner, King's College

21.00–22.00 THE CONSEQUENCES OF MAPPING THE FLORA OF EUROPE

(Illustrated talk in Keynes Hall, King's College)

Dr F. H. Perring, Monks Wood Experimental Station

Monday, 1 July

09.00–18.00 EXCURSION TO SALTMARSH, FEN AND BOG COMMUNITIES OF NORFOLK

Leaders: Mr R. P. Libbey, Mr P. D. Sell, Mr E. L. Swann

19.30 Dinner, King's College

21.00–22.30 RECEPTION in Fitzwilliam Museum at inauguration of exhibition of botanical illustration from the Broughton Collection

Tuesday, 2 July

09.00–17.00 EXCURSION TO MONKS WOOD EXPERIMENTAL STATION, INCLUDING THE BIOLOGICAL RECORDS CENTRE, AND WOODWALTON NATURE RESERVE

Leaders: Dr S. M. Walters, Dr F. H. Perring, Mr M. Schofield

19.30 Dinner, King's College

HISTORY OF THE BRITISH CONTRIBUTION TO THE STUDY OF THE EUROPEAN FLORA

William T. Stearn

A conference on floristic studies in Europe must necessarily be international both as regards its participants and its subject-matter. My allotted task for this Conference has been to provide a cursory survey of the British contribution to these studies. The contribution of any one nation to knowledge of the European flora cannot, however, be considered entirely apart from the work of others, because plants attained their ranges under the influence of factors by no means the same as those which have determined modern national boundaries; hence they often extend across them, thereby being made vegetable citizens of more than one country. Moreover, modern botany has been an international science from its very beginning. Work on the plants of one country has so often become relevant to those of others that botanical scholars have always tried to keep abreast of the contributions of their fellow-workers elsewhere, examining, assessing, criticizing, using and appreciating them according to their merits; in this way all these botanists have increased and shared a common inheritance of knowledge. Their work collectively manifests the cultural unity of Europe.

Situated in the north-western corner of Europe, Britain possesses, on account of its Atlantic climate and its greatly varied topography, a diversity of plants less common elsewhere in northern Europe; the British contribution to European floristic studies has been based primarily upon these but has certainly not been confined to them. It began in the sixteenth century when botany developed as an independent study out of herbalism, being an outgrowth of enquiry into vegetable *materia medica*. It pushed forward under the general questioning spirit and dissatisfaction with the immediate past which then found its theological expression in the works of Erasmus and Luther and its scientific expression in those of Copernicus, Galileo, Vesalius and lesser men. Among these men was William Turner (1508–68), the ‘father of English botany’.

The area in which modern botany originated has been indicated on a map published by Isaac Henry Burkill (1870–1965) in 1953 and included in his posthumous *Chapters on the History of Botany in India* (1966). On his map (Fig. 1) Burkill marked all the places at which

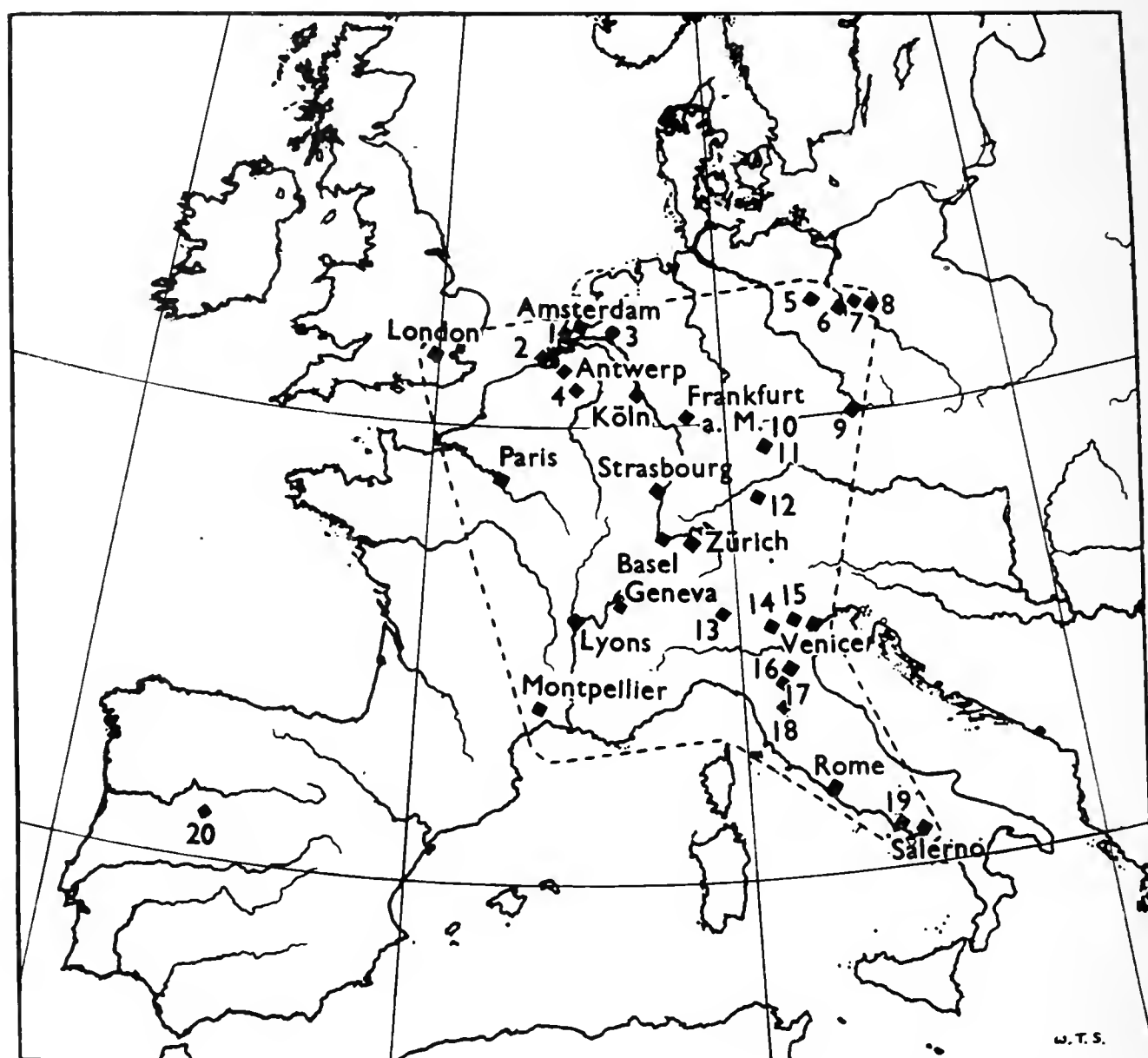


Fig. 1. The area in which modern botany originated (based on Burkill, 1953). Places named are those where three or more botanical books were printed between 1500 and 1623. Numerals indicate places where one or two botanical books were printed: 1. Leyden; 2. Middelburg; 3. Arnhem; 4. Louvain; 5. Berlin; 6. Leipzig; 7. Bautzen; 8. Görlitz; 9. Prague; 10, 11. Nürnberg and nearby Altdorf; 12. Augsburg; 13. Bergamo; 14. Mantua; 15. Padua; 16. Ferrara; 17. Bologna; 18. Florence; 19. Naples; 20. Salamanca. Bologna under Luca Ghini and Montpellier under Rondelet were important centres of botanical teaching.

(Reproduced from *Proc. Linnean Soc. London*, 169: 179 (1958) by courtesy of the Linnean Society of London.)

botanical books were printed between 1500 and 1623, the year of Gaspard Bauhin's *Pinax*; this important work listed virtually all the plants then known, with their numerous synonyms, and was compiled from virtually all the books then published. The area encompassing their places of publication stretches from Salerno in Italy northward to London, with an out-station at Salamanca in Spain. At this period, as Burkill noted, the printing of a book at a given place is reasonable evidence of its having been written in the neighbourhood and also of enough interest there to justify its printing. The delimited area covers

territory occupied by the Dutch, English, French, Germans and Italians, but Latin provided them with a common language. Because of the close association of botany with medicine, those universities having the highest repute for medical teaching, Padua and Montpellier, influenced most the development of botany. Students from distant lands, going to them for anatomical and other medical instruction, learned the new technique of herbarium-making invented by Luca Ghini and the old classical names of plants as interpreted by their teachers. These two universities owed their sixteenth-century eminence to a spirit of enquiry which could flourish only in a tolerant or at least non-hostile academic environment such as is more commonly associated with a trading and manufacturing community than with a purely academic or ecclesiastical one. Money was money for the Venetian republic, of which Padua was the university, whatever the race, creed or beliefs of those providing it. *Pecunia non olet*.

WILLIAM TURNER

For England, indeed for the British Isles, botany began with William Turner, 'unquestionably the earliest writer among us, that discovered learning and critical judgment in the knowledge of plants', as Pulteney said in 1790. His *Libellus de Re herbaria* (London, 1538) and the *Names of Herbes in Greke, Latin, Englishe, Duche and Frenche* (London, 1548) are the first two printed books relating to the British flora which have any claim to originality. Only two copies of the first and less than twelve of the second are known to have survived, their format being too humble to ensure careful preservation, but they are available in a low-priced facsimile, with extensive introductory matter, published by the Ray Society in 1965. Turner followed these in 1551–68 with *A New Herball*, which is fortunately not so scarce. His aim was essentially medicinal, to equate English vernacular names of plants with Latin equivalents and thereby to make such plants available as *materia medica*. Thus incidentally he recorded for the first time some 238 species of British plants. The publication of his works implies a public for them in England; indeed, Turner himself stated in 1538, with probable exaggeration, that 'there are six hundred of us Englishmen who in this kind of learning would precede me (as the saying goes) on white horses'.

Turner was a doughty Protestant controversialist, the author of such books as *The Huntyng and Fyndyng out of the Romyshe Fox*, which in the troubled sixteenth century meant the risk of being burnt as a heretic (which Turner, unlike his friends Thomas Ridley and Hugh Latimer, escaped through his second exile), and of having one's publications banned, confiscated and burnt, which happened. His

Libellus (1538) shows him to have been acquainted with the works of Ruel and Brunfels. In 1540 he and his wife found it prudent to leave England and go into exile. His wanderings took him up the Rhine, his wife probably being left at one of the Rhineland cities where English exiles congregated, and into Italy, where he certainly visited Venice, Ferrara and Bologna, studying here under the great teacher and reluctant writer Luca Ghini; he also visited Milan and Como; thence he went to Switzerland, crossing the Alps to Zürich, here meeting Conrad Gessner, then going to Basel and down the Rhine to Cologne. Presumably here he rejoined his wife; their son Peter was born in 1542. They later settled in East Friesland, Turner there serving the Earl of Emden as his physician, then moved into the Low Countries. After the death of Henry VIII in 1547, Turner returned to England and became physician to the Protector Somerset at Syon House across the Thames from his own garden at Kew. In 1548 he published his *Names of Herbes* which contains many references to plants seen on his continental travels, and in 1551 the first part of his *New Herball*. The accession of Queen Mary in 1552 and the consequent persecution of Protestants caused Turner, his wife and their three young children to leave England again for the safety of Germany, and he did not return again until the accession of her Protestant half-sister Queen Elizabeth I in 1558. He died in 1568. The influence of these enforced travels on the continent of Europe upon Turner's publications from 1548 onwards is very evident in the references he makes to plants growing there. They indicate correlation between the plants of England and elsewhere. Thus Turner, through his direct acquaintance with continental plants, literature and botanists, brought British botany from the start into the main stream of European botanical learning.

The major contribution which any scholar could make then to the floristic botany of Europe was to record the plants of his homeland. Turner did not, however, set out to record all the plants of England; his aim was to provide correct names for those that could be used in medicine, the same intent as that of his contemporaries Euricius Cordus and Leonhart Fuchs. According to W. A. Clarke, *First Records of British Flowering Plants*, 2nd ed. (1900), his works contain notices of 238 native flowering plants. Since his interest was primarily medicinal, they include few grasses and no sedges but many members of the Compositae and Umbelliferae. The association of scientific names with vernacular names undoubtedly aids the popularization of botany: Turner recorded such English names as he knew and, when none existed, he proposed names of his own, writing as he was 'unto the English my countremen an Englysh herball'. Thus of the herb called by herbalists *Saponaria* and grown in German gardens he remarked that

‘I never sawe it in England, therefore I know no englishe name for it. However if we had it here, it myght be called in english sopewurt or skowrwurt.’ Thus *Saponaria officinalis* acquired its English name Soapwort. Similarly he proposed that the herbarist’s *Pyrola* ‘maye be called in englishe wyntergrene’ and that *Larix* ‘maye be called in englishe a Larche tree’.

Turner’s most important immediate successor was Matthias de l’Obel (1538–1616) from Flanders, the author of *Plantarum seu Stirpium Historia* (1576) and physician to William the Silent. He settled in England about 1586 and lived here until his death. Clarke credits him with no less than 80 first records of British plants. De l’Obel, who is commemorated by the genus *Lobelia*, had a hand in the preparation of John Gerard’s *Herball* (1597). This added 182 species to the British list. Thus, as Clarke pointed out, by 1600 about 500 species of British plants were known and described and most had been correlated with those of the Continent; they included 21 grasses and three sedges.

THOMAS JOHNSON AND THE SOCIETY OF APOTHECARIES

Turner had collected much information about British plants on his travels in England. Early in the seventeenth century medical men and apothecaries began to make deliberate ‘public excursions and simpling-tours’ in order to acquaint themselves at first hand with medicinal and other plants. These botanical excursions became a regular activity of the Society of Apothecaries soon after they had dissociated themselves in 1617 from the Grocers’ Company and become an independent body ‘Corporate and Politic’ with a charter from King James I. The best documented journeys are those of Thomas Johnson (1604–44) and his friends because he published accounts describing their travels and finds. In 1629 they made a trip into Kent, followed by one to Hampstead Heath, described in Latin in Johnson’s *Iter Plantarum Investigationis...in Agrum Cantianum Anno Dom. 1629...Ericetum Hamstedianum* (1629). In 1632, they made a longer Kent journey described in Johnson’s *Descriptio Itineris Plantarum Investigationis...in Agrum Cantianum Anno Dom. 1632* (1632). These two rare booklets are now available in a facsimile, together with translations and commentaries, edited by J. S. L. Gilmour (1972). Such excursions were evidently jovial, as well as scientific, and educational, and the Society of Apothecaries continued them down to 1834, which resulted in the flora of the London region’s being fairly well recorded before its extermination or reduction by urban development. Some excursions extended to fifty miles from St Bartholomew’s Hospital or Apothecaries’ Hall, London, the usual meeting places. For 55 years they were conducted

by Thomas Wheeler (1754–1847), a teacher much esteemed both for his geniality and learning. He remained an active field botanist while in his seventies and possessed a profound knowledge of grasses, sedges, rushes, umbellifers and Compositae as well as of less critical groups. On these excursions, when over 70, he wore a threadbare black coat and breeches and long leather gaiters. It is related by Field and Semple that on one occasion, when the party was returning in an open coach near Maidstone, Wheeler sat on the box beside the driver,

with his hat off, his thin light hair blowing about his face and his large spectacles on his nose, alternately laughing and chatting with the driver and diving into his hat with his huge pocket-knife, separating and examining a bundle of wild plants. Such a figure naturally attracted attention along the road, and when stopping at a turnpike-gate, the party were rather surprised by the evident interest and eagerness of the toll-keeper, as he scratched his head, and, pointing to Mr. Wheeler, exclaimed in his blunt Kentish dialect, ‘So ye ha’ got him at last!’ This was incomprehensible to all the party until they arrived at a small inn close to the parish of Barming, where they read a placard offering a reward for the capture of an escaped lunatic!

The American botanists John Gill Lemmon and his wife Sara, collecting plants where Indians were on the warpath, later owed their lives to being similarly identified through their addiction to such a mad activity.

In 1634 the Apothecaries led by Johnson made an even longer journey, going to Bristol, by way of Reading, Marlborough and Bath. The most important of their journeys, however, was to North Wales in 1639, by way of Chester, Holywell, the Great Orme’s Head, Aberconway, Bangor and Caernarvon, ascending Snowdon on the 3rd of August, then to Machynlleth and Montgomery, and back to England, through Ludlow, Hereford, Gloucester and Oxford. Edward Morgan, one of the party, was a Welshman. Without him as an interpreter their journey, difficult enough on account of the wildness of the ways through the mountains, might have yielded little on account of linguistic difficulties and suspicion of strangers by its equally wild inhabitants, who in fact treated them very hospitably, as they later did Willughby and Ray, the latter making the remark, ‘The Welch people generally are extremely civil and well bred, very honest and courteous to strangers’.

Johnson’s purpose in making such journeys and listing the plants found was to assemble material for a complete descriptive account of British plants in collaboration with his friend John Goodyer (1592–1664), who was no such traveller, but a diligent, scholarly and sharp-eyed student of Hampshire plants, described in 1657 as ‘the ablest Herbarist now living in England’. The Civil War of 1642–6 tragically brought their plan to nothing. Johnson joined King Charles’s forces at Oxford and fought as a Royalist in the defence of Basing House near Basingstoke

during its long siege by Parliament forces; here he died in September 1644 from a gunshot wound received during a sortie. The production of a much-amended edition of Gerard's *Herball* in 1633, which remained a standard work well into the eighteenth century and became known as *Gerardus emaculatus*, and the accounts of his travels with their lists of plants stand to his credit. In these he recorded some 170 species as new for the British flora.

THE INTERREGNUM, 1640–67

The death of so enthusiastic and learned an apothecary and field botanist as Johnson at the age of 40 was a bad but not fatal blow to British botany at a time when interest in it was steadily growing. Others, though not of the same ability, kept it alive. Thus six years later William How produced *Phytologia Britannica* (1650), an uncritical compilation based on Johnson's *Mercurius botanicus* (1634) but containing new records from How's friends, which was popular because there existed nothing better. This added 16 species to the British list.

How died in 1656 before he could produce a new edition, but his publisher obtained the services of a physician, Christopher Merrett (1614–95). Merrett could not travel much himself, but he did the best he could in getting additional information. Thus he employed an old soldier, Thomas Willisel, used to rough living and travel on foot, uneducated but with a keen eye for plants, and sent him every year for five years on collecting trips all over England. In 1666 Merrett published a *Pinax Rerum naturalium Britannicarum*, with a second edition in 1667; this added 46 species. Among his friends was William Harvey, famous for his work on the circulation of the blood, but also keenly interested in botany, and thus characteristic of the many British physicians and apothecaries who provided a public for such books on British plants. Merrett took some material from John Ray's *Catalogus Plantarum circa Cantabrigiam nascentium* (1660), a little book which Charles Raven has described as 'initiating a new era in British botany'.

JOHN RAY

A conference in Cambridge on European floristic botany can honour no man more fittingly than John Ray (1627–1705), who travelled widely both in Britain and on the Continent for the study of plants and whose works in the seventeenth century provided a foundation for those of Linnaeus in the eighteenth. Ray, like Linnaeus, was of humble rural origin, his father being a blacksmith at Black Notley, Essex. He

received, however, a good education at the grammar school in nearby Braintree and, supported by a Braintree scholarship for 'hopeful poor students' of 'sober and Christian conversation', he entered the University of Cambridge in 1644, the year of Thomas Johnson's death. He graduated B.A. in 1647/8, was appointed Greek lecturer in 1651, mathematical lecturer in 1653, and humanities lecturer in 1655 and was ordained as a clergyman in the Church of England in 1660. Botany had then no official place in university education at Cambridge, but there existed nevertheless a group which studied it for their own private interest. Ray's own study began in 1650 when convalescence from illness gave him leisure to examine the plants growing around Cambridge, aesthetic delight leading on, as it so often has, to critical research into their characteristics and differences. In 1654 a young nobleman Francis Willughby (1635–72) became his pupil. Their friendship blossomed into a fruitful scientific collaboration which ultimately enabled Ray to devote all his time to natural history. In 1660 he published his *Catalogus Plantarum circa Cantabrigiam nascentium*, a list of the plants growing around Cambridge, preparatory to a list of those of Britain as a whole. This was intended to replace How's *Phytologia Britannica*; 'to which purpose', he told Willughby in 1660, 'I am now writing to all my friends and acquaintance who are skilful in Herbary to request them this summer to search diligently his country for plants and to send me a catalogue of such as they find, together with the places where they grow'. Thus began the co-operative recording, area by area, of the distribution of British plants. This culminated in the nineteenth century in the publication of two works by Hewett Cottrell Watson (1804–81), *Cybele Britannica* (1847) and *Topographical Botany* (1873), followed in the twentieth century by F. H. Perring and S. M. Walters, *Atlas of the British Flora* (1962) based on one and a half million field records contributed by some 1,600 collaborators, most of them amateur botanists.

This enquiry by Ray led to his *Catalogus Plantarum Angliae* (1670) and that to his *Synopsis methodica Stirpium Britannicarum* (1690). These works rested upon a first-hand acquaintance with the British flora gained by extensive travel as well as by extensive correspondence. Thus in 1660 Ray and Willughby journeyed to the north of England and over to the Isle of Man. In 1661 Ray and Philip Skippon went to Scotland, travelling along the eastern side of England by way of Lincoln, Harrogate, York, Newcastle, Berwick, to Edinburgh, then westward to Glasgow and by way of Carlisle and the Lake District back to Cambridge. In 1664 Ray and Willughby made a journey through Wales and the south-west of England. Such travel involved much discomfort and some danger, but Ray, Skippon and Willughby were unique only

in undertaking it for the study of natural history; many a gentleman and occasionally even a young lady such as the courageous and inquisitive Celia Fiennes set out then to visit the great houses, the remains of antiquity, and the market towns, to note the manufactures and general state of their country.

The habit of touring their native land [states Esther Moir in her *The Discovery of Britain*] began in the sixteenth century: it is a Tudor phenomenon...the motive force was pride in the greatness of Tudor England, and a curiosity both in the historic roots of that greatness and its contemporary manifestations. Bound by no tradition or convention, lacking the established routes and rituals of the Grand Tour, it became a popular pastime amongst gentlemen of leisure to travel for weeks, even months, in the discovery of their own country.

The roads they traversed were mostly appalling, rough in dry weather, deep with mud and treacherous in wet weather, sometimes 'little better than ponds of liquid dirt with a scattering of loose flints just sufficient to lame every horse that travelled them', as Arthur Young described Wiltshire roads, and the flea-infested inns were often little better as regards comfort. Enthusiasts like Ray and Willughby took such discomforts and hazards as a matter of course in getting to know the natural history of their native land.

In all Ray, with the aid of his friends and correspondents, added some 200 species to the British list. These helpers were numerous (cf. Stearn, 1973, pp. 34–41) and among the most enthusiastic of them was a young Welsh scholar, Edward Lhwyd (1660–1709), who not only searched Snowdon for rare plants, finding among them *Lloydia serotina*, *Cerastium arcticum* and *Isoetes lacustris*, but also lesser mountains and hills, including Craig Breiddin (his 'Craig Wreidhin') in Montgomeryshire, where he discovered *Potentilla rupestris* and *Veronica spicata* subsp. *hybrida*. The contemporary rendering of his surname as 'Lloyd', 'Floyd', 'Lhuyd' and 'Luidius' may be confusing. The natural son of an eccentric and dissolute squire Edward Lloyd and a Caernarvonshire gentlewoman Bridget Pryse, he retained the usual anglicized patronymic 'Lloyd' (whence the generic name *Lloydia* commemorating him) until about 1686, then adopted with antiquarian zeal the older Welsh spelling 'Lhwyd' (grey), which he latinized as *Luidius* to accord with the pronunciation of 'Lhwyd'. The university of Oxford and Jesus College, Oxford having inexplicably refused after his death to purchase his many volumes of notes and drawings relating to the natural history and antiquities of Wales and Ireland, these passed into private hands and were destroyed in two disastrous fires, but botanical specimens from him are preserved in the British Museum (Natural History) and Oxford herbaria (cf. Clokie, 1964; Dandy, 1958).

The big crisis in Ray's life came in 1662 with the enforcement of the

pernicious Act of Uniformity; rather than assent to this, which implied that an oath was not binding, some 2,000 clergymen of the Church of England forfeited their livings and among them was Ray, with the prospect before him of extreme poverty and frustration. Willughby came to his aid and by thus freeing him for research and travel made possible his further immense contribution to European botany. Together they had travelled many thousands of miles around England and Wales. In 1663 they set out on a Continental tour lasting until 1666, which took them through the Low Countries, Rhineland Germany, Austria, Italy, Switzerland and France and out to Sicily and Malta. No botanist before, except Clusius, had had the opportunity of acquiring so wide a knowledge of European plants, and Ray made full use of it. Willughby died prematurely at the age of only 36, leaving an annuity to Ray, which enabled him to devote most of his life thereafter to preparing the works on birds, fishes, insects and plants they had planned together. The most massive of these was his *Historia Plantarum* in three thick folio volumes (1686, 1688 and 1701), which incorporates the results of their European travels. This work and Dillenius's edition (1724) of Ray's *Synopsis methodica Stirpium Britannicarum* constitute a very important contribution to European floristic botany and have a lasting value because of the information they provided Carl Linnaeus (1707–78) when preparing his *Species Plantarum*. From the *Synopsis* Linnaeus derived most of his knowledge of the occurrence of species in Britain. The *Historia* gave him details about distribution in Europe generally. Thus Linnaeus stated that *Epimedium alpinum* 'habitat in Alpium Euganeorum, Ligurinorum, Ponteborum umbrosis'. This information came from Ray's *Historia Plantarum* 2: 1330 (1688), where Ray states that he himself had observed the plant 'non longe a Ponteba oppido quod territorium Venetum et Imperiale disternat'.

In 1754 Linnaeus published a dissertation, *Flora Anglica*, which attempted a correlation of the Swedish and British floras by applying binomial names to the plants listed in the *Synopsis* (1724), which used, of course, pre-Linnaean phrase-names (cf. Stearn, 1973, pp. 42–68). His 'Caput Quartum' deals concisely with the history of botany in Britain. Here he noted that at the beginning of the seventeenth century the English nation seemed little fitted for, and indeed almost alien to, the study of botany, whereas by its end they had produced as many botanists as the whole of Europe, and among these Ray stood at the head.

As a result of their combined efforts, by 1700 some 970 species of flowering plants were known from Britain; collecting and study by their successors in the eighteenth century raised this to about 1,145 by 1800.

GENERAL CONTRIBUTION

The work of Ray illustrates three of the five main kinds of contribution that botanists of a given country can make to the floristic botany of Europe as a whole.

I. The investigation of the plants of their own country, defining and naming its species and ascertaining their distribution and ecology, is exemplified by Ray's *Catalogus Plantarum circa Cantabrigiam nascentium* (1660), his *Catalogus Plantarum Angliae* (1670) and his *Synopsis methodica Stirpium Britannicarum* (1690, 1696). Such investigation has often brought to notice species hitherto unknown but later found elsewhere.

The type-locality of a species is the place whence came the material on which the protologue of its name is based. When this is merely stated in broad terms such as 'Europa', 'India', 'Nova Hollandia', it may nevertheless be possible to make this more precise by ascertaining such information as the name of the collector, his routes and collecting areas, or by excluding the areas from which no material could be available at the time of publication. A locality thus delimited within a wider area originally designated has become known, particularly among ornithologists, as the 'restricted type-locality'. Thus the restricted type-locality for *Geranium lucidum* L., of which Linnaeus gave the distribution as 'Habitat in Europae rupibus umbrosis', is Torsburg on the island of Gotland, where Linnaeus collected it on 3 July 1741 (cf. *Biol. J. Linn. Soc.* 5: 7-9 (1973)).

A remarkably large number of species were first named from British material, thanks to the work of Ray, Miller, Hudson, Sibthorp, Curtis, J. E. Smith, Babington and others. Species with their type-locality in Britain include:

<i>Hymenophyllum tunbrigense</i> (L.) Smith	<i>Rhynchosinapis wrightii</i> (O. E. Schulz) Dandy
<i>Asplenium viride</i> Hudson	<i>Cochlearia alpina</i> (Bab.) H. C. Watson
<i>Cystopteris dickieana</i> Sim	<i>Cochlearia micacea</i> E. S. Marshall
<i>Woodsia alpina</i> (Bolton) Gray	<i>Cochlearia scotica</i> Druce
<i>Dryopteris pseudomas</i> (Wollaston) Holub & Pouzar	<i>Cochlearia anglica</i> L.
(<i>D. borrieri</i> (Newman) Tavel)	<i>Cardamine flexuosa</i> With.
<i>Ranunculus circinatus</i> Sibth.	<i>Arabis brownii</i> Jordan
<i>Meconopsis cambrica</i> (L.) Vig.	<i>Viola lactea</i> Smith
<i>Fumaria occidentalis</i> Pugsley	<i>Viola lutea</i> Hudson
<i>Fumaria purpurea</i> Pugsley	<i>Hypericum elodes</i> L.
<i>Rhynchosinapis monensis</i> (L.) Dandy	<i>Cerastium nigrescens</i> Edmondston ex H. C. Watson

- Cerastium pumilum* Curtis
Sagina maritima Don
Sagina boydii F. B. White
Herniaria ciliolata Melderis
Chenopodium ficifolium Smith
Chenopodium botryodes Smith
Atriplex glabriuscula
 Edmondston
Halimione pedunculata (L.)
 Aellen
Arthrocnemum perenne (Miller)
 Moss
Salicornia dolichostachya Moss
Salicornia ramosissima Woods
Salicornia pusilla Woods
Tilia cordata Miller
Malva pusilla Smith
Linum bienne Miller
Genista anglica L.
Trifolium ochroleucon Hudson
Trifolium dubium Sibth.
Trifolium occidentale Coombe
Vicia orobus DC.
Potentilla fruticosa L.
Potentilla anglica Laich.
Rubus microspecies (more than
 110)
Alchemilla conjuncta Bab.
Alchemilla minima Walters
Rosa arvensis Hudson
Rosa sherardii Davies
Sorbus microspecies (about 15)
Sedum anglicum Hudson
Sedum forsterianum Smith
Umbilicus rupestris (Salisb.)
 Dandy
Ribes spicatum Robson
Drosera anglica Hudson
Physospermum cornubiense (L.)
 Burnat
Berula erecta (Hudson) Coville
Oenanthe fluviatilis (Bab.)
 Coleman
Ligusticum scoticum L.
Euphorbia portlandica L.
Polygonum minus Hudson
Rumex hydrolapathum Hudson
Rumex palustris Smith
Ulmus glabra Hudson
Ulmus procera Salisb.
Salix nigricans Smith
Limonium humile Miller
Limonium binervosum (G. E.
 Smith) C. E. Salmon
Limonium recurvum C. E. Salmon
Limonium transwallianum (Pugs-
 ley) Pugsley
Limonium paradoxum Pugsley
Primula scotica Hooker
Primula vulgaris Hudson
Centaureum latifolium (Smith)
 Druce
Centaureum littorale (D. Turner)
 Gilmour
Gentianella anglica (Pugsley)
 E. F. Warb.
Verbascum virgatum Stokes
Euphrasia microspecies (about
 14)
Calamintha sylvatica Bromf.
Galeopsis speciosa Miller
Scutellaria minor Hudson
Phyteuma tenerum R. Schulz
Senecio cambrensis Rosser
Arctium pubens Bab.
Carduus tenuiflorus Curtis
Hieracium microspecies (more
 than 100)
Alisma lanceolatum With.
Eriocaulon aquaticum (Hill)
 Druce
Polygonatum odoratum (Miller)
 Druce
Scilla verna Hudson
Juncus castaneus Smith
Luzula forsteri (Smith) DC.

<i>Luzula sylvatica</i> (Hudson) Gaudin	<i>Carex spicata</i> Hudson
<i>Allium ampeloprasum</i> L.	<i>Carex curta</i> Gooden.
<i>Narcissus obvallaris</i> Salisb.	<i>Carex ovalis</i> Gooden.
<i>Epipactis purpurata</i> Smith	<i>Carex pauciflora</i> Lightf.
<i>Epipactis leptochila</i> (Godf.) Godf.	<i>Festuca pratensis</i> Hudson
<i>Epipactis dunensis</i> (T. & T. A. Stephenson) Godf.	<i>Festuca tenuifolia</i> Sibth.
<i>Epipactis phyllanthes</i> G. E. Smith	<i>Puccinellia maritima</i> (Hudson) Parl.
<i>Ophrys apifera</i> Hudson	<i>Puccinellia rupestris</i> (With.) Fernald & Weatherby
<i>Ophrys sphegodes</i> Miller	<i>Catapodium rigidum</i> (L.) C. E. Hubbard
<i>Orchis purpurea</i> Hudson	<i>Poa flexuosa</i> Smith
<i>Dactylorhiza fuchsii</i> (Druce) Soó	<i>Poa balfourii</i> Parnell
<i>Dactylorhiza praetermissa</i> (Druce) Soó	<i>Poa subcaerulea</i> Smith
<i>Dactylorhiza purpurella</i> (T. & T. A. Stephenson) Soó	<i>Bromus erectus</i> Hudson
<i>Eleocharis multicaulis</i> (Smith) Smith	<i>Bromus ramosus</i> Hudson
<i>Carex laevigata</i> Smith	<i>Brachypodium sylvaticum</i> (Hudson) Beauv.
<i>Carex binervis</i> Smith	<i>Agropyron donianum</i> F. B. White
<i>Carex extensa</i> Gooden.	<i>Hordeum marinum</i> Hudson
<i>Carex sylvatica</i> Hudson	<i>Helictotrichon pratense</i> (Hudson) Pilger
<i>Carex depauperata</i> Curtis ex With.	<i>Deschampsia setacea</i> (Hudson) Hackel
<i>Carex rostrata</i> Stokes	<i>Calamagrostis scotica</i> (Druce) Druce
<i>Carex riparia</i> Curtis	<i>Agrostis setacea</i> Curtis
<i>Carex pendula</i> Hudson	<i>Agrostis tenuis</i> Sibth.
<i>Carex strigosa</i> Hudson	<i>Alopecurus myosuroides</i> Hudson
<i>Carex disticha</i> Hudson	<i>Spartina maritima</i> (Curtis) Fernald
<i>Carex divisa</i> Hudson	
<i>Carex divulsa</i> Stokes	

This list does not include names based on British material which have passed into synonymy because the species concerned had earlier been described on the Continent. Thus *Bromus britannicus* I. A. Williams (1929) was found to have been earlier described in Sweden as *B. lepidus* O. R. Holmberg (1924), although its recognition as a species hitherto unnoticed in Britain reflected great credit on that enthusiastic, cultured and sharp-eyed amateur botanist Iolo Aneurin Williams. Inclusion of taxa now commonly given infraspecific rank and first detected in Britain, e.g. *Sparganium neglectum* Beeby (= *S. erectum* subsp. *neglectum* (Beeby) Schinz & Keller), *Veronica humifusa* Dick-

son (= *V. serpyllifolia* subsp. *humifusa* (Dickson) Syme), would also have lengthened the above list.

II. The second kind of contribution is that made by botanists visiting countries other than their own and diligently collecting material for study. Here Ray had a predecessor in Thomas Penny (c. 1530–88), like Turner and Ray a Cambridge scholar. In 1565 he turned from theology to medicine and went to Zürich; here he met Conrad Gessner, to whom he gave drawings and specimens of British plants. He also corresponded with Clusius and gave him drawings reproduced in his *Rariorum aliquot Stirpium per Pannoniam Historia* (1584) and *Rariorum Plantarum Historia* (1601). These include *Anemone narcissiflora* found in the Jura near Geneva and *Rubus chamaemorus* from Ingleborough ('Engelborow') in Yorkshire, but the most interesting of his finds is that called *Myrto-cistus pennaei* by Clusius, 'ex Balearium insularum majore, vulgo Majorica nuncupata', which is now *Hypericum balearicum*, and probably the first species recorded from the Balearic Islands. There being no terminal y in Latin, Clusius referred to Penny as 'Thomas Pennaeus, Londinensis medicus'.

The main British collecting effort of the last century was, however, made outside Europe, in the expanding British Empire, notably in Australia and India, and led to such important works as W. J. Hooker's *Flora Boreali-Americana* (1829–40), Grisebach's *Flora of the British West Indian Islands* (1850–64), Bentham's *Flora Australiensis* (1863–78), J. D. Hooker's *Flora of British India* (1872–97), etc. Nevertheless, material gathered on short trips and holidays by a diversity of persons and now in the British Museum, Cambridge, Edinburgh, Kew, Manchester and Oxford herbaria, particularly from Spain, Italy and the Balkan peninsula, has provided a valuable basis for much work on the *Flora Europaea*. Such specimens have included new species. *Centaurea ebenoides*, for example, was discovered on Euboea by the English philosopher and economist John Stuart Mill when touring Greece in 1862.

III. A third contribution is the preparation of Floras or regional lists. Here again Ray made a notable contribution by including so many European records in his *Historia Plantarum* derived from his own travels as well as from the literature. The major British activity in this has been, as indicated above, outside Europe and has borne fruit not only in the major Floras mentioned but also in smaller works such as Bentham's *Flora Hongkongensis* (1861), Gamble & Fischer's *Flora of Madras* (1915–36), Dalzell & Gibson's *Bombay Flora* (1861), J. L. Stewart's *Punjab Plants* (1809), Haines's *Botany of Bihar and Orissa* (1921–4), Theodore Cooke's *Flora of the Presidency of Bombay* (1901–3), Duthie's *Flora of the Upper Gangetic Plain* (1903–29), Prain's *Bengal*

Plants (1903), Trimen's *Handbook of the Flora of Ceylon* (1893–1900), etc., some of these covering areas as big as many European countries. The British contribution to European regional Floras has been essentially the work of well-informed and enthusiastic amateurs, among the first being Bentham's *Catalogue des Plantes indigènes des Pyrénées et du Bas-Languedoc* (1826) followed by P. B. Webb's *Iter Hispaniense* (1838), J. H. Moggridge's *Flora of Mentone* (1867), Clarence Bicknell's *Flora of Bordighera* (1896) and A. H. Wolley-Dod's *Flora of Gibraltar and the Neighbourhood* (*J. Bot., Lond.* 52: Suppl. (1914)).

The most notable British contribution to a European Flora is, however, Sibthorp and Smith's *Flora Graeca* (1806–40). John Sibthorp travelled in Italy, Greece, Asia Minor and Cyprus from 1784 to 1787 accompanied by the young botanical artist Ferdinand Bauer, who made superb drawings of the plants seen to illustrate a Flora of Magna Graecia. Sibthorp died in 1796, leaving illustrations, muddled notes and income from the Sibthorp estate for the publication of a *Flora Graeca* in ten volumes. Thanks to the devoted care of his executor Thomas Hawkins, the engraving of the plates by James Sowerby and the preparation of the text for Vols. 1–7 part 1 by James E. Smith and for Vol. 7 parts 2–10 by John Lindley, publication of this magnificent and costly work was achieved in 1840, the original edition reaching only 25 complete sets, each of which cost about £620 to produce, though sold at £254. Between 1845 and 1856 Henry Bohn published a re-issue of about 40 copies. The total cost of the undertaking was £15,572 (cf. Stearn, 1967).

IV. A fourth kind of contribution is the preparation of monographs embracing all the European species. In general, British botanical effort has been directed to the preparation of Floras of British overseas possessions rather than of monographs covering other areas. Here again George Bentham stands out by his work *Labiatarum Genera et Species* (1832–6), but the most remarkable are George Maw's *Monograph of the Genus Crocus* (1886), and W. R. Dyke's *The Genus Iris* (1912), based on years of study of living plants assembled in their gardens. Neither *Crocus* nor *Iris* can be studied satisfactorily from dried material. They are, however, groups of considerable horticultural value with a high aesthetic appeal, and as such have attracted the painstaking attention of an especially British type, the gardener-botanist, whose particular characteristic is to take up a group of garden interest, collect and cultivate together all the available kinds, study their characteristics in a living state and, after years of intimate acquaintance with them, produce a handbook, survey or revision. J. G. Baker, originally a draper, then a botanist in the Kew Herbarium, did useful work in revising the Liliaceae in a long series of papers in the *J. Linn. Soc.*,

Bot. 11–18 (1870–80). More recently (1941–50) W. W. Smith and H. R. Fletcher have published a series of papers in the *Trans. Proc. bot. Soc. Edinb.* 33–5 (1941–50), *J. Linn. Soc., Bot.* 52 (1942) and *Trans. R. Soc. Edin.* 50–1 (1942–3) revising section by section the genus *Primula*.

V. From these regional floras and world monographs it is one step forward to the major synthesis, the Flora of all Europe, *Flora Europaea*. Grisebach attempted such a work but achieved only a fragment published in 1882. Werner Rothmaler put forward plans for a *Flora Europaea* in 1944, but it is undeniable that the major impetus and most of the money for this great international work have come from the British Isles. Throughout its preparation taxonomists in every part of Europe have contributed advice, constructive criticism and accounts of genera. Contributors to Vols. 1–3 number 125. Of these Britain has provided 60, Germany and Czechoslovakia each 7, Portugal and Switzerland 5, Poland and Spain 4, France, Austria and Hungary 3, fourteen other countries 1 or 2. The work is thus part of the British contribution to European floristic botany, but it is also a European contribution to British floristic botany. Such fruitful interaction has its roots in the sixteenth century. The international membership of the present conference on European floristic botany in Cambridge is evidence of its happy continuance and growth.

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FLORISTIC STUDIES IN GREECE

W. Greuter

ABSTRACT

A historical survey of the floristic exploration of Greece, followed by some suggestions for an effective and harmonious international collaboration. The present state and future prospects of Greek floristics are illustrated by four maps.

Dr Stearn has spoken to us about the contribution of a single nation, Great Britain, to the botany of Europe. The lecture I have been asked to give deals with a fairly complementary subject: the exploration of the flora of a single country, Greece, by students from all over Europe. Let me state from the very beginning that this survey of the floristic exploration of Greece can by no means aim at completeness. I had to attempt to operate a selection and, at the same time, some sort of classification of the countless contributors to Greek floristics. A strictly chronological sequence did not seem very satisfactory to me. I have adopted thematical headings which coincide to a fair extent, however, with particular though partly overlapping chronological periods.

1. THE CLASSICS

One can find several good reasons for the choice of Greece, in preference to other countries, as a subject for this lecture – beginning with the trivial one that it is the region with which I am most familiar, and ending with the statement that no other part of Europe exemplifies to such a striking degree the past and present interwovenness of floristic research all over Europe, irrespective of political boundaries. But the most valid of arguments, at least on an emotional level, is that Greece is rightly considered the birthplace and cradle of scientific botany.

Theophrastos (372–287 B.C.), born at Eressos on the East Aegean island of Lesbos (Mitilini), was Aristotle's most famous student and his successor as a head of the Peripatetic school at Athens. He was a philosopher in the most comprehensive sense of the word, his interests ranging from metaphysics and politics to the natural sciences.

It happens that one of his few works to have survived is the *Histories on plants* (περὶ φυτῶν ἱστορίαι). This incredibly fascinating, genial text brings scientific botany into existence and raises it, at the same time, to a level of perfection which was not to be reached again for about two thousand years. The roots (and more than the sheer roots) of most of the modern disciplines of botany can be found in the *Histories on plants*, namely systematics, morphology, anatomy, phyto-geography and ecology.

Still better known than Theophrastos's masterly treatise, and with a much more immediate impact on the further development of botany, is a later work of a very different kind: the *Materia medica* (περὶ ὕλης ἰατρικῆς) of Pedanios Dioskorides. This Greek from Asia Minor (born in Anazarbos in Cilicia), an army doctor under Nero, lived in the first century A.D. The scope and intent of his work was an eminently practical one: it is a sort of handbook, giving a review of the very impressive professional knowledge of the widespread and highly esteemed school of Greek herbalists and physicians. Much of its contents, obviously, is existing tradition forged into a new frame; but some parts – as, for example, the synonymies in many contemporary languages – appear to be original and due to Dioskorides's wide range of knowledge and experience.

Theophrastos and Dioskorides are names which stand for many others: botanists and herbalists whose works are more obscure, partly or entirely lost. Doubtless botany – together with all other fields of science and philosophy – reached a first and very marked climax in ancient Greece. Through the Byzantine Empire, the medieval monastic scholarship and some Arabic and other sources, a few sparks and sprinkles of this venerable and admirable tradition have been saved for us; as to the remainder, we are left to imagine what it may once have been.

2. THE HUMANISTS

The return to the classical sources which characterized the Renaissance period favoured the onset of the botanical exploration of Greece. The old Greek and Latin plant names of Dioskorides and Pliny had been currently applied to a variety of Central and North European species by the medieval herbalists. It was now felt that these interpretations needed a severe reappraisal: the original sources were again to be used, and checked against the plants growing in the classical countries, first of all Greece.

At the beginning of this new trend stands a very rare book on the simples and their interpretation, written by Luigi Anguillara (1561), who

had himself visited Italy and the Balkans, down to the island of Crete, on the tracks of the ancients. He was followed by many others, some of them prominent naturalists like Tournefort and Sieber (see section 4). John Sibthorp is a prominent example who, before setting out on his Greek expedition, thoroughly studied a world-famous, beautifully illustrated copy of Dioskorides: the 'Codex Aniciae Julianae', a Byzantine manuscript dating back to A.D. 512, kept at the Imperial Library at Vienna. Sibthorp's contribution to Greek botany is a very prominent one which Dr Stearn has outlined in his paper on the British contribution to European floristics (see also Stearn, 1967).

Karl Fraas (1845) published a book which represents both a masterly synthesis of and a conclusion to the humanistic investigations of the Greek flora. His *Synopsis plantarum florum classicae* is a compendium of the plant names of the classics with their modern equivalents, resulting mainly from the author's own, extensive Greek field studies. Fraas was, between 1838 and 1843, the first professor of botany of Athens University, then newly founded by King Otho I. His departure coincided with the dismissal of all foreign (specifically Bavarian) state ministers and higher officials, which was enforced by a Greek rebellion. This is just one of many examples of the strong interrelation between politics and floristics, and leads us to say some words on Greek political history.

3. THE HISTORICAL BACKGROUND

This is in fact an extremely complex and manifold subject, and only a very generalized, rudimentary picture can be given here. Following the fall of Constantinople and the dismemberment of the Byzantine Empire (1453), Greece was taken over by the Turks and by Venice. The former gradually widened their domain, first to the whole continental area whose conquest was virtually achieved in 1460 (except for a few harbours), then to the islands: Rhodes fell in 1522, Crete in 1669 and Tinos as late as 1715. Only the Ionian Islands remained Venetian up to the French Revolution, and were afterwards transformed into a British protectorate.

Greek national independence had thus to be won at the expense of the Turks. This was achieved in the Greek liberation war (1821–9), succeeded by the establishment of a Greek kingdom under the Bavarian prince Otho in 1832. This kingdom originally comprised Central Greece, the Peloponnese, Euboea and the Cyclades, and was later gradually extended to its present shape and size: in 1864 the Ionian Islands were handed over by Britain, in 1881 Thessaly and the Arta province became Greek; the Balkan Wars led to the annexation, in 1913, of Epirus,

Macedonia, Crete and the East Aegean islands; in 1923, after the conclusion of the rather catastrophic Greco-Turkish war, western Thrace was added; finally, as a result of World War II, the Dodecanese was taken over from the Italians, who had occupied it since 1912.

When considering the historical development of Greek floristics, one must acknowledge the fact that the Greek (and, earlier, the Venetian) parts of the territory were much more easily accessible than the Turkish domain. Especially the inland areas under Turkish administration were far from safe: political instability, corruption and inefficiency of local administrations, tribal wars and brigandage made travelling in those countries troublesome and dangerous. The means of inland communication were also rudimentary, while sailing was relatively safe. Thus, most of the early botanical explorers of the Ottoman provinces travelled by sea and concentrated on the islands and some coastal regions of the mainland; indeed, the only Greek mountain areas which had been botanically explored to a satisfactory extent, prior to the 1830s, were those of Crete.

4. THE NATURALISTS

The early explorers of the Greek flora were no thoroughbred botanists: they displayed a wide range of interests in natural history, geography, ethnography, archaeology and the humanities. The country was so unexplored in every respect that one could hardly afford to concentrate on a single, specialized subject at that time: everything was new and noteworthy and had to be investigated, gathered and published. Travel reports from the sixteenth to the nineteenth century are fascinating reading, although the information they convey lacks many details, and sometimes even accuracy.

The first prominent example of a naturalist to explore Greece was the French Pierre Belon du Mans. During his travels to the Levant, in 1546 and 1547, he visited Crete, the North Aegean islands Lemnos and Thasos, Mt Athos, the coastal areas of eastern Macedonia and Thrace and the islands of Lesbos, Hios, Samos, Patmos, Kos and Rhodes in the eastern Aegean. His observations were published in the form of a highly informative and original book (Belon, 1553), whose French text was subsequently translated into Latin by Charles de l'Ecluse.

Another Frenchman, Joseph Pitton de Tournefort, explored Crete and a considerable number of the smaller Aegean islands in 1700, together with the painter Aubriet and a German doctor, Gundelsheimer. This expedition is particularly important to us since Tournefort's primary interest was in plants: he was Professor of Botany at the Paris Muséum, and author of a skilful and highly esteemed plant system. His

thorough knowledge of the vegetable kingdom and of its classification enabled him to digest rationally the huge quantity of material he found and collected, and to allot their proper places to the many new species he discovered. The general account of his travels was published posthumously, in the form of letters, together with some beautiful copper engravings of the most notable plant species (Tournefort, 1717).

A further most readable travelling report is that of Franz Wilhelm Sieber (1823) who had explored Crete in 1817. Captain (and later Rear-Admiral) Dumont d'Urville's Aegean cruise in 1819 yielded only a purely botanical account (Urville, 1821).

The next notable enterprise was due to the French habit (initiated by Napoléon Bonaparte on his Egyptian campaign) of connecting scientific and military expeditions. France had despatched an army corps to the Peloponnese (the Morée, as they called it) during the later stages of the Greek War of Independence. This was paralleled in 1829 by the 'expédition scientifique de Morée' under Colonel Bory de Saint-Vincent, who later edited the results in an impressive multi-volume series (*Botanique* by Fauché *et al.* 1832–6).

The newly created Greek kingdom with its safer travelling opportunities attracted many students, especially Germans. Among the authors of corresponding narratives, some had a marked interest in botany: Emanuel Ritter von Friedrichsthal (1838), the 'Bergkommissar' Karl Gustav Fiedler (1840–1) and the well-known Viennese paleobotanist Friedrich Unger (1862) may be cited in this context.

August Grisebach deserves a special mention: he was the first to defy the dangers of the mountainous inland regions of the still Turkish portions of the Balkans. He crossed northern Greece in 1839, coming from Constantinople: from the Evros estuary he went to Maronia, crossed to the island of Thasos and to Mt Athos, continued through the Halkidike peninsula to Thessalonica, Edessa and Arnissa and ascended Mt Kajmakčalan or Vorras (Nidže planina); he afterwards visited the now Yugoslavian part of Macedonia, climbed Mt Pelister and the Šar planina and, having cut across northern Albania, finally reached the Austrian territory of Montenegro. The whole journey is very nicely described in his two-volume report (Grisebach, 1841).

A French geographer and geologist, Victor Raulin, scanned Crete very thoroughly in 1845, collecting plants which were partly determined by Boissier. His masterly treatise on the island (Raulin, 1869) includes a sizeable chapter on botany, based on both his own and Heldreich's results (see the next section).

Last but not least among the naturalists, Forsyth Major – mainly known as a vertebrate paleontologist – collected plants on several Aegean islands between 1886 and 1890, sponsored by Boissier's son-

in-law William Barbey at Geneva. From these expeditions two monographic works on the natural history of Samos and Karpathos resulted (de Stefani *et al.* 1892, 1895).

5. THE FIELD BOTANISTS

From approximately 1840 onward, the naturalists were gradually replaced by explorers with purely botanical interests. Specialization had become a real necessity if further progress was to be achieved. It made it possible to investigate the subject in a much more thorough manner, to collect more material and, above all, to convey more accurate and much more detailed information about this material thanks to an improved labelling procedure. There are, of course, exceptions, but in general one can say that the naturalists' specimens are valuable only as historical documents (and often as nomenclatural types), while those collected by the botanical explorers can serve as a reliable base for floristic records and distribution plots.

Edmond Boissier, the well-known author of the *Flora orientalis* (1867–88), was the father and initiator of Greek field botany. Having visited Greece himself in 1842, he convinced a virtually unknown young German botanist to settle in Athens and to start exploring the different regions of the country. This talented youngster was to stay in Greece for almost 60 years, from 1843 to his death in 1902, and to become the most famous and knowledgeable botanist who ever resided in this country. His name was Theodor von Heldreich.

Heldreich's contribution to the development of Greek botany can hardly be overrated. Apart from his official duties (he was director of the Athens Botanical Garden from 1851 to 1902, and keeper of the Natural History Museum from 1858 to 1883), he made innumerable collecting expeditions and excursions all over Greece, of which only the most important can be mentioned: to the Peloponnese in 1844, to Crete in 1846 and again in 1870, to the Thessaloniki area and Mt Olympus (then still Turkish) in 1851, across the Central Greek mountain areas in 1879 and to the freshly annexed territory of Thessaly in 1882, 1883 and, together with Haussknecht, in 1885. Moreover, Heldreich was invaluable as an adviser, mentor and sometimes companion to other field botanists and professional collectors. His activity resulted in the discovery of a great number of new species (mostly described together with Boissier), of innumerable new plant localities, and in classical, widely distributed sets of exsiccata of which the *Herbarium graecum normale* is the best known (see Halácsy, 1902).

Eduard Formánek, from Brünn (now Brno) in Bohemia, was one of those fearless explorers who defied the Turks, the fierce natives

and the brigands of the Balkan interior. On several journeys between 1889 and 1899 he visited, apart from many areas of present-day Yugoslavia, the now Greek western Macedonia, Thessaly and Epirus. His botanical skill and care were not, alas, equal to his courage and perseverance: his specimens were poor, and his determinations even worse, so that his various floristic papers are best ignored. It is fortunate that Vandas (1909) revised critically the whole Formánek collection, so through his book the many interesting new records are now safely available.

As unwearied and intrepid a traveller as Formánek, and a much better botanist and collector, was Antonio Baldacci of Bologna. Best known as explorer of Albania, he made significant contributions to Greek botany too, visiting the Epirus in 1892, 1895 and 1896, and Crete in 1893 and 1899. Even in the latter already rather well-known area he made several interesting finds owing to his predilection for unusual itineraries and remote spots (see, e.g., Baldacci, 1895, 1903, 1917).

Eugen von Halácsy, an Austro-Hungarian physician and botanist, is most famous as the author of a flora of Greece (Halácsy, 1900–8, 1912) which is still, in my judgement, the best of its kind, in spite of its age and of the fact that its boundaries exclude most of the more recent Greek territories like Macedonia, Thrace and the eastern islands. Halácsy acquired his own Greek field experience on three journeys in 1888, 1893 and 1911, of which the second was the most important. It led through Epirus, Thessaly, Aetolo-Acarmania and the northern Peloponnese and yielded a series of very thorough floristic accounts (Halácsy, 1894).

An equally important series of papers resulted from the Greek expeditions of René Maire in 1904, 1906, 1908 and 1917 (the second one together with M. Petitmengin). They are important for both phanerogamists and cryptogamists, especially mycologists, to whom René Maire's name is a very familiar one indeed (see Maire, 1906–9, 1922). Incidentally, the original set of specimens from these trips is not in the Maire herbarium, now deposited at Montpellier (MPU), but at the Faculty of Sciences of Nancy University (NCY).

Other familiar names of botanists who visited Greece are Michel Gandoger (in Crete from 1914 to 1917, possibly with some kind of pseudo-diplomatic or secret service activity; see Gandoger, 1916, 1919, 1920); Johann Bornmüller in 1926 (Bornmüller, 1928; he had already visited Mt Athos in 1891, together with Sintenis); and Peter Davis, who travelled extensively on the islands and the continent in the early stages of World War II, prior to the German occupation, and visited Crete and Karpathos again in 1950 (see Davis, 1953, 1955).

Several Bulgarians (e.g. Urumov, Stojanov, Stefanov, Kitanov; see

Kuzmanov, 1971, for further details) made basic contributions to the knowledge of the flora of northern Greece, although their publications have been somewhat neglected because they are written in Bulgarian, and many of them are not readily available. One may remember that parts of Macedonia and Thrace were Bulgarian from 1912 to 1918, and again occupied by Bulgarian forces during World War II.

In recent times Greek field botany has been very much intensified. Improved travelling facilities and stable political conditions are partly responsible for this development. But we must not forget the persons who are behind this general trend, and first of all Karl Heinz Rechinger who, having first visited Greece in 1927, has been backsliding fairly regularly to this sin of his youth – at least twenty times up to the present day. His main attention was devoted to the islands and peninsulas of the Aegean sea (Rechinger, 1943, 1949, 1961), and notably to Crete, which he visited with a German wartime scientific expedition in 1942 (Rechinger, 1944; a parallel expedition led Rothmaler to the Peloponnese, but the collected materials were destroyed at Berlin, following an Allied air raid, before being worked up). Several excursions to the mainland, from Peloponnese to Epirus and Thrace, must also be mentioned, but only two of them yielded floristic accounts (Rechinger, 1936, 1939).

Rechinger's are certainly by far the most extensive Greek collections ever brought together by a single person. They are outnumbered, however, by those made by a collective enterprise which one may call the Lund undertaking, or Runemark's team: a group of young Swedish botanists who have been scanning one by one all the countless islands of the Aegean, from 1957 onward (Runemark *et al.* 1960–74), and are now doing the same with the mountain peaks of the mainland. Once all the results of this collecting are available in a published form, we will be justified in stating that the preliminary chapter of the floristic investigation of Greece has been successfully closed.

6. THE PROFESSIONAL COLLECTORS

The contribution of plant dealers and professional collectors to Greek floristics is far from negligible. They have certainly set new standards in the techniques of collecting and drying plant specimens. Unfortunately their labels are not always prepared as carefully as the corresponding exsiccata. In a few cases (Reverchon!), they are indeed so carelessly prepared that one could easily speak of fakes...

We find forerunners of the 'professionals' in the first half of the nineteenth century, with Sieber in Crete in 1817 (see section 4), Frivaldszky's hired collectors in Crete and northern Greece, and

Aucher-Eloy in Attica, on Mt Athos and on some islands. But the high periods of professionalism were the second half of the nineteenth century – with names such as Balansa, Bourgeau, Pichler, Reverchon and Sintenis – and the early years of our century: Adamović, Dimonie, Dörfler and Leonis. Apparently the First World War settled the fate of this profession: plant dealing is no longer, it seems, financially rewarding.

7. THE GROUP EXCURSIONS

Collective excursions are an invention of our century. Today, commercial tourist cruises with partly naturalistic aims are current and very popular, especially in Britain, but originally such group excursions were the prerogative of universities.

The first to make a group attack on Greek botany were the Viennese, who organized two 'Universitätsreisen' in 1911 and 1914; Zürich followed in 1921, under the leadership of Martin Rikli and Eduard Rübel. Nowadays, almost every year botanical university excursions swarm over Greece. They are not usually of a basic importance to floristic research: they tend to follow trodden paths, mostly around touristic centres with hostels and opportunities for bathing, shopping and archaeological sight-seeing. To some extent, this seems to have been true even for the pioneer enterprises mentioned above, if we believe what Samuelsson (1933) wrote on the subject of the Zürich excursion in which he had participated (translation mine): 'Unfortunately I had in a way misunderstood the purpose of this trip – it turned out to be to a large extent of a purely touristic nature, with a pronounced tendency to swallowing kilometres – and had also over-rated the knowledge of the leader (Rikli) with respect to the Mediterranean flora...'

As a rule, the scientific results of group excursions are not published. In some cases, duplicated plant lists are produced, often with rather provisional determinations. The Vienna and Zürich travels, however, yielded extensive scientific reports which belong to the traditional Greek floristic literature (Vierhapper, 1914–16, 1914–19; Rikli & Rübel, 1923). A more recent example is the International Phytogeographical Excursion to Greece in 1971, whose results will be published shortly (Dafis & Landolt, 1975).

8. THE AMATEURS

The amateurs have actually and chronologically succeeded the naturalists – indeed, in a way, they *are* naturalists, just denoted by a less ambitious term. The amateurs' contribution to Greek floristics was a very prominent one, although it is still imperfectly known since most of their results remain unpublished. It is very difficult, if not impossible, to keep a record of botanical amateur activity in Greece, especially during these last few years since tourism has so tremendously increased. Citing any names, in this context, would mean being unfair to the many equally prominent amateur botanists left unmentioned. (By the way, I am proposing no special category for trained botanists on their holiday trip, without a specific Greek research programme, who may just as well be included together with the amateurs.)

There are, however, three persons who must be specifically mentioned here. They owe this special treatment to the fact that they have all been living in Greece for a long time: Shirley Atchley and Fernand Guiol in Athens, from where they have explored many and often remote parts of the country; and H. G. Tedd in Xanthi who has mainly investigated western Macedonia, Thrace and the northern Aegean area. Guiol's herbarium is now at the British Museum (Natural History), and Atchley's and Tedd's are at Kew. All three are rich in new, mostly unpublished findings which certainly deserve to be put on record.

9. THE PHYTOSOCIOLOGISTS

They are the youngest members of the big family of Greek botanists – but certainly not the most unproblematic ones. The good botanical amateur, as we have just seen, can be characterized as a remarkable collector, a keen connoisseur of plants, but a very lazy author. Conversely, one might depict the phytosociologists – even some of the best! – as poor collectors with an inadequate floristic knowledge, but with a tremendous printed output.

After this slightly disrespectful statement (for which I apologize to all those colleagues – and they exist indeed – who do not deserve it), I will certainly be forgiven for not dwelling on this subject and for not giving any concrete examples. But I want to make it quite clear that data from phytosociological relevés (and in a few cases, alas, even from floristic publications by a phytosociologist) should not be recognized as floristic records unless specimens have been checked.

10. THE GREEK BOTANISTS

Having begun our survey with the Greek fathers of botany, we have been lingering on several categories of students from abroad. It is now time, as a conclusion, to revert to the genuine Greek botanists.

The first to gain well-deserved reputation and fame in this field was Theodoros Orphanides, Fraas's successor in the Chair of Botany of Athens University which he held from 1849 to 1882. Orphanides was successful both as a botanical explorer and as a scientist, collaborating with Boissier and Heldreich but also working independently. He distributed a well-known series of exsiccata on an exchange basis, and assembled a considerable world-wide personal herbarium which now constitutes the main body of the Athens University herbarium.

After Orphanides' retirement, floristics and systematic botany practically disappeared from the Greek universities, the botanical professors concentrating on other fields of research, or on teaching activities (see Phouphas, 1940). Some successful collecting was done in the early years of our century by the successor of Heldreich at the Athens Botanical Garden, B. Tountas. We must proceed to the 1930s to find a renewed, though still timid, rise of our discipline in Greece, mainly centred on Thessalonica University where Konstantinos Ganiatsas, who was to become Professor of Botany and a very successful teacher of plant systematics, began publishing a series of valuable floristic contributions.

Today, of the several chairs of botany at the three Greek universities only one, at Patras, is occupied by a phanerogam taxonomist: Dimitrios Phitos, well known for his skilful and thorough contributions to floristics and cytotaxonomy. But there is a striking renewal of interest in the subject at the other botanical institutes too, and several young students and scientists are now enthusiastically proceeding to the exploration of the floristic riches of their home country.

11. THE GREEK AMATEURS

Greece too has had, and still has, some prominent amateur botanists. To begin with, we may mention Miss Sophia Topali, whose specimens are now at the Geneva Conservatoire botanique (G). Her main area of activity was Mt Pelion, close to Volos in Thessaly where she was living. She also visited other parts of Greece, partly together with Gustave Beauverd, the keeper of the Boissier Herbarium (see Beauverd & Topali, 1937). She was executed during the German occupation in World War II, being suspected of collaboration with the Greek partisans.

Two of the most sizeable Greek herbaria, each of about 25,000

specimens, have been built up in fairly recent times by local amateurs. Both are of considerable importance to the student of the Greek flora, since they contain unpublished and inadequately studied material often collected in remote, ill-known areas whose access even nowadays remains difficult. The first is due to the skill of Leonidas Pinatzis: it is a beautiful, remarkably well-arranged collection, still kept and cared for by his family. The second has been assembled by Constantine Goulimis, a specialist of international and commercial law who, having decided at the age of sixty to devote himself to the plant life of Greece, ceaselessly explored all the parts of this country from 1946 to his death in 1963. His herbarium contains innumerable new findings and many novelties, a few of which were described and published by Turrill & Rechinger (see also Goulimis, 1956, 1960; Goulandris, Goulimis & Stearn, 1968); it is now at the Goulandris Natural History Museum whose foundation, in fact, was directly motivated by its bequest.

12. THE GOULANDRIS MUSEUM

This institution, which was founded in 1964 in Kifisia near Athens as a botanical museum and was later expanded to include other branches of natural history as well, has the status of a private foundation made and endowed by Mr and Mrs Angelos Goulandris. By now it plays a major role in Greek botany. It has its own collecting staff: the most active collaborators are Mrs Elli Stamatiadou, who is a very keen and gifted plant hunter and has been successfully prospecting the whole country since 1967; and Paul Haristos, who lives in Thessalonica and has been concentrating on the flora of Macedonia from 1971 onward. On the other hand, a scientific library is now being built up, publication activity has started and several research programmes, monographic as well as floristic, are under way. The Goulandris Museum has also prepared a public exhibition in order to increase the knowledge and love of nature of the Greek population, and above all of the young generation who will have to resolve the increasingly urgent problems of the conservation and management of nature and the human environment.

Besides its own activity as a centre for public education, collecting, documentation and research, the Goulandris Museum sees one of its most important and noble tasks in the establishment and maintenance of contacts between the many students of Greek botany, and in a co-ordination of their efforts. It serves as a strengthening point and working base to many botanists, including the amateurs who have been largely neglected by the university institutes. It favours the exchange of information and aims at establishing a correlation between the independent research programmes of different students and teams.

Most urgently, it endeavours to strengthen and improve the relations between Greek and foreign botanists.

13. THE PROBLEMS OF INTERNATIONAL COLLABORATION

The Greek botanists, quite naturally, tend to have an inferiority complex when faced with the numerous foreign specialists successfully working in their home country, having a training, an experience and – last but not least – domestic research facilities such as libraries and herbaria which cannot yet be obtained within Greece. This feeling of frustration usually turns into blank fury when it appears that those foreign botanists have been working, and are publishing, in their personal research fields, without giving them the slightest chance of knowing beforehand and of delimiting appropriately the respective subjects.

I believe that we must understand these reactions, and try to prevent them. Incidentally, they are by no means limited to Greece, but widespread in most or all the so-called developing countries. Unfortunately in many cases – not yet in Greece! – they have led not only to a regrettable general animosity against foreign research but, more concretely, to deplorable and counter-productive administrative restrictions to scientific activity, especially to fieldwork.

Faced with similar problems in Central and South America, a group of biologists from the United States has produced a sort of chart of good behaviour for biologists abroad, which is basic reading for all those, amateurs and especially professionals, planning fieldwork in foreign countries: no severe, weary rules, just some self-imposed imperatives and restrictions which, at a first glance, seem so self-commendatory to a decent-minded scientist that it is hard to believe how often one has unconsciously neglected them in the past. These 'Guidelines for biological field studies' have been reprinted in *Taxon* (19: 950–1 (1970)), and I should like to forcibly recommend everyone who has not yet done so to study them carefully, paying special attention to the seven points of the second section dealing with 'guest scientists'. The establishment of close contacts with colleagues of the host country, the exchange of information, materials and publications and the co-ordination of research are essential prerequisites for a fruitful international collaboration.



Map 1. The floristic investigation of Greece. A, well or reasonably well explored areas. B, ill-explored areas. C, unexplored areas. Further explanations in the text. (The inset in the left-hand bottom corner of this and the following maps represents the Greek island group of Kastellorizo off the S. Anatolian coast.)

14. THE PRESENT STATE OF THE FLORISTIC EXPLORATION OF GREECE

A report on this topic by W. Greuter, D. Phitos and H. Runemark was recently presented at the CNRS Colloquium on the 'Flore du bassin méditerranéen' (Montpellier, 4-8 June 1974). Its conclusions were summarized in the form of four maps which are reproduced here. The complete report will be published in the Proceedings series of the 'Colloques internationaux du CNRS'; it will include literature



Map 2. An estimate of the relation of published to unpublished floristic information in Greece. A, areas from where more than two-thirds of the available information has been published. B, areas from where one-to-two-thirds of the available information has been published. C, areas from where less than one-third of the available information has been published.

references relating to map 3, and details concerning the research projects of map 4.

Map 1 is based on an overall estimate of the total amount of available information, both published and unpublished (such as herbarium specimens and reliable field notes). Islands and mainland areas where an estimated 80 per cent of the existing wild species, or more, have been collected or noted are considered to be 'reasonably well explored'. Most of the other regions are 'ill-explored', the exceptions being a few small islands and some mountains at the Albanian and Bulgarian



Map 3. Greek areas covered by recent floristic publications (see the text for additional explanations). A, thorough coverage (by a comprehensive study or several minor contributions). B, incomplete coverage.

frontiers which, to my knowledge, have never been visited by a botanist or collector. Although the criteria applied are less severe on the mainland (the 'areas' considered there are, on average, much bigger than the individual islands), it is obvious from the map that the insular parts of Greece were much more thoroughly explored than the continent and especially its lowlands.

Map 2 shows to what a considerable extent the available floristic information on Greece is still unpublished, and is designed as a warning not to rely on printed sources only when dealing with the

Macedonia and Thrace and Halácsy (1900–8, 1912) for the remainder of Greece.

It is hoped that this set of maps, imperfect as it is, will contribute to a rationalization of future floristic activity, and entail an increased effort to investigate the still imperfectly known or unexplored Greek areas.

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APOMIXIS IN A STERILE HYBRID SPECIES OF *POTENTILLA*

R. Czapik

ABSTRACT

Hexaploid *Potentilla mixta* Nolte (= *P. reptans* f. *mixta* Krause = *P. anglica* Laich. \times *P. reptans* L.) from England and Poland is highly sterile. It reproduces, however, abundantly by runners which show morphological seasonal variation in special conditions. A few seeds developed by some clones after open pollination were raised to plants of various ploidy level ranging from $5x$ to $9x$ ($2n = 35, 42, 56, 63$) and a single individual with c. $93-7$ chromosomes. Cytological differentiation of the progeny is connected with a tendency to apomixis of the maternal plants. Thus the reproduction of *P. mixta* represents a complicated system of vegetative propagation, sexuality and apomixis covered by the sterility of the hybrid taxon.

In this paper I shall try to present some of the special problems we meet in highly sterile hybrids of a genus rich in apomictic taxa.

Polymorphism, apomixis and polyploidy are combined in *Potentilla* with comparatively often noted interspecific hybridization. The taxon was engaging a good deal of attention in the works of Müntzing (1928–58), Rutishauser (1943–67), Hunziker (1954), Smith (1963 *a, b*), Smith, Bozman & Walters (1971), Asker (1966–71) and many others who studied cytology, embryology, apomictic phenomena and their regulation, as well as intraspecific variability.

There is one basic number $x = 7$ in the genus. The euploid numbers range here from 14 to 112. Several numbers are recorded in certain species which comprised euploid and aneuploid plants and in a few cases also plants with fragments of chromosomes. The aneuploids which are rare in nature are noted very often among experimental plants from inter- or intraspecific crosses. The occurrence of aneuploids shows that gametes with aberrant chromosome numbers are able to function in *Potentilla*, and aneuploid plants may survive in special conditions.

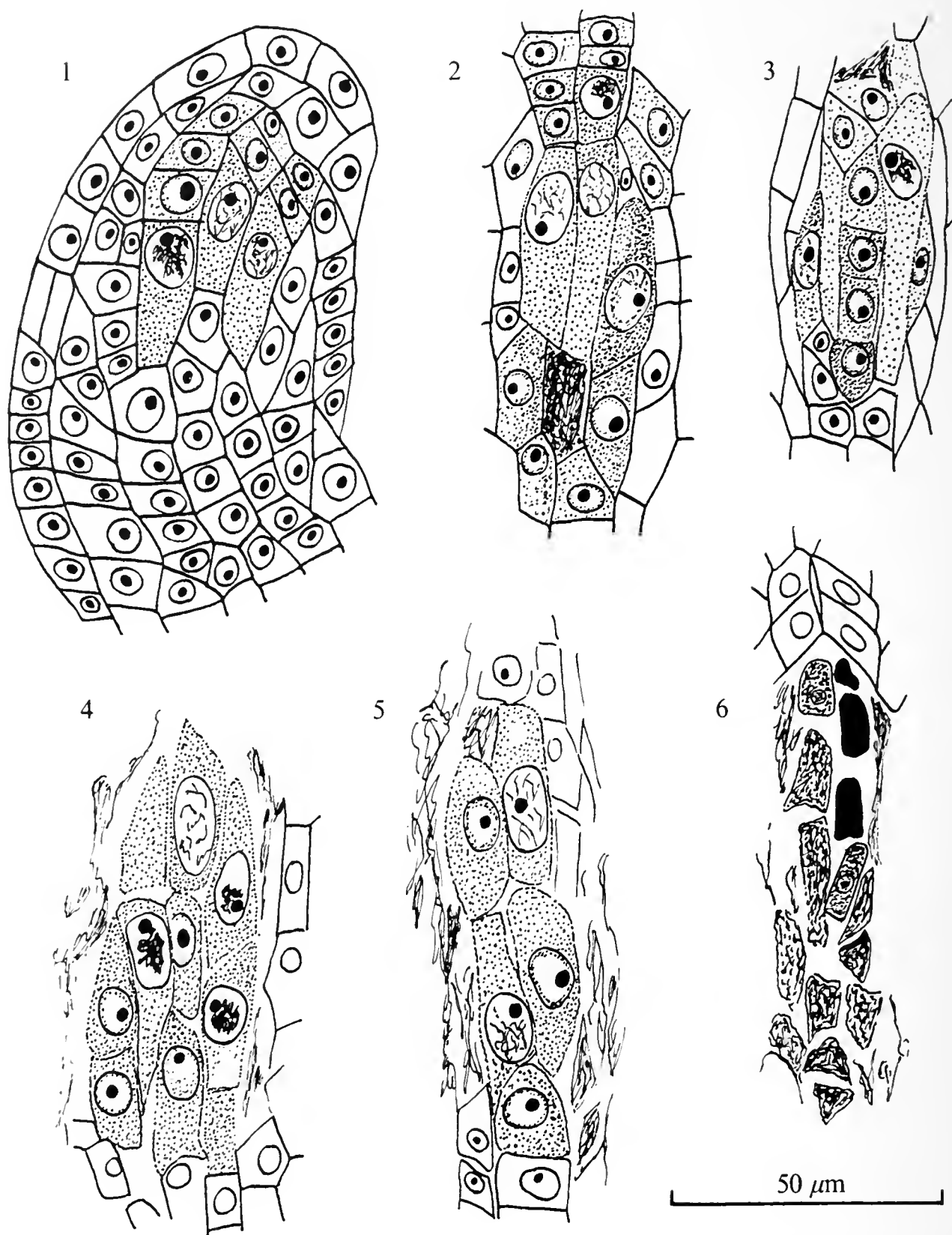
In spite of the fact that in published records polyploid apomicts prevailed there is no simple correlation between the degree of polyploidy and apomixis in *Potentilla* on account of the complicated and still

not well recognized genetic regulation of the apomictic processes. On the diploid level apomixis is determined by independent systems of recessive genes, which cause the elementary apomictic processes; apospory, diplospory and parthenogenesis (Rutishauser, 1967; Asker, 1971). The genes have a quantitative effect. The systems of apomictic genes were resistant toward the mutagenic treatment of X-rays and ethyl methane sulphonate in experiments of Asker (1966 *a*). However, they may be broken down or restored as a result of hybridization or polyploidization.

Most of the apomictic *Potentillas* belong to the pseudogamous group and require fertilization of the central nucleus for the development of endosperm and a viable seed. Single fertilization which occurs in pseudogamous plants is not the only element of sexuality in apomictic *Potentilla*. They are as a rule facultative apomicts. Both diplosporous as well as aposporous plants may develop unreduced and reduced embryo sacs in various percentages, and their egg cells may be fertilized. In the progenies of these facultative apomicts triploid and diploid hybrids occur among matroclinous plants. Thus polymorphism in *Potentilla* is in the first place connected with this special mode of reproduction apart from hybridization and some cytological mechanisms which seem to act occasionally in the course of developmental processes (Asker, 1966 *b*, 1971).

According to the last review of apomixis done by Khokhlov in 1967 apomixis was recorded in 30 species of *Potentilla*, and since then at least three further examples may be added to this list. Among those taxa 19 species belong to the European representatives of the genus. This rather high number of noted apomictic species is in some way connected with the attractiveness of the genus for students, but it is still low in comparison with the number of unexamined taxa.

To classify a plant as an apomict many data are needed. The embryological examination reveals the origin of young embryo sacs and degree of apomeiosis as well as early development of autonomically parthenogenetic embryos. The frequency of functional embryo sacs with reduced and unreduced chromosome number in facultative apomicts may be established only after cytological and morphological analysis of progenies, obtained after several controlled pollinations with plants which have various chromosome numbers and belong to various taxa. The examination of progeny from open pollination or from one cross only is insufficient. According to the experiments of Rutishauser the degree of pseudogamy and the number of fertilized unreduced egg cells depends on the pollen plant used in a cross. Such a complex investigation meets additional obstacles in the case of highly sterile hybrids.



Figs. 1-6. Archesporium and initial cells in *P. × mixta*. 1, young ovule (stage II) at the beginning of meiosis; 2, archesporium and aposporous initial cells; 3, tetrad; 4, meiosis arrested in early prophase; 5, diplosporous initial cells; 6, degenerated tetrad.

The sterile natural and experimental hybrids in *Potentilla* were not embryologically examined. There were, of course, observations on meiosis in anthers and degree of pollen and seed sterility. However, histological backgrounds of the seed sterility are unknown. There are no remarks about the reproductive tendencies interrupted by the sterility. Let us see some aspects of such an investigation using the example of *P. × mixta*.

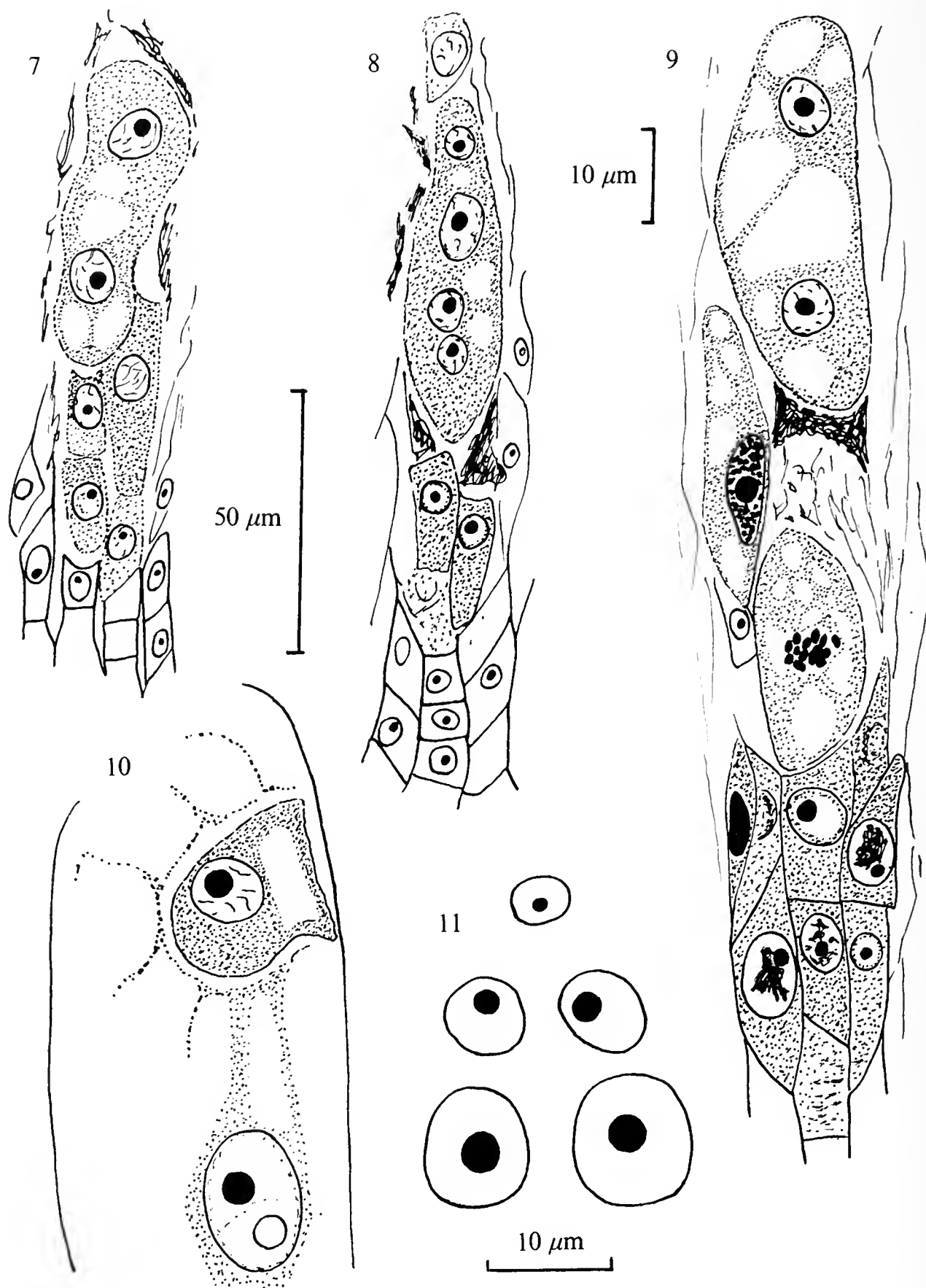
P. × mixta Nolte ex Reichenb. shows the characteristics of the genus: polyploidy and morphological variability together with a hybrid origin. Typical *P. × mixta* has 42 chromosomes and is believed to be a complicated hybrid of the group *Tormentillae*, highly sterile but reproducing abundantly by runners. In its genetic constitution four genomes of *P. reptans* and two of *P. erecta* are involved. So the domination of *P. reptans* in many characters of *P. × mixta* is understandable.

The hybrid might originate from a successful pollination between *P. reptans* and *P. anglica* (the latter is a stabilized hybrid of *P. reptans* and *P. erecta*), or directly from a cross between *P. reptans* and *P. erecta*. In the last case a hexaploid *P. × mixta* would be formed as a consequence of the fusion of a tetraploid gamete of *P. reptans* with a diploid gamete of *P. erecta*. The experimental confirmation of one of these ways was done by Matfield, Jones & Ellis (1970). The authors obtained two plants morphologically similar to natural *P. × mixta* from the cross of octoploid (autoploid) *P. reptans* as the maternal plant with a tetraploid *P. erecta*, the pollen plant. They mentioned also a synthesized hexaploid *P. × mixta* obtained by Valentine from the cross *P. reptans* as the maternal plant and *P. anglica* as the pollen plant.

It is interesting to mention that Schwendener (1969) obtained two hybrids after pollination of a tetraploid *P. reptans* with tetraploid *P. erecta*. The plants had 42 and 44 chromosomes respectively and originated, as the author assumed, from unreduced gametes of *P. reptans* fertilized by reduced gametes of *P. erecta*. The ploidy level and genetic constitution especially of the euploid hybrid seemed to be in accordance with the expected constitution of *P. × mixta*. Nevertheless, both experimental plants show morphological similarities to *P. anglica* in their habit and branching.

We know rather little about the variability of *P. × mixta*. The examples from Monks Wood showed, for instance, a seasonal variation in the shape of leaves in some degree connected, among other possible factors, with variable watering. Three types of runners differing in shape and size of leaves, presented in the paper of Matfield *et al.* (1970) for three different plants, were developed by the same individuals from Monks Wood. On the other hand the plants from two other localities in Poland, Rybnik and Muzaków (Czapik, 1968) did not show such striking morphological changes.

The high sterility of *P. × mixta* is the main obstacle in successful pollination experiments. The degree of sterility varies within the population and within the same specimen, but it is always very high. In the experimental field some plants did not develop any seeds after open pollination during several years, but others had 0–3 seeds in one flower. Most of these seeds were, however, empty, only 9–11 per cent



Figs. 7–11. Embryo sacs of *P. × mixta*. 7, binucleate ES; 8, abnormal four-nucleate ES; 9, two uni- and one binucleate ES, cells arrested in the I prophase; 10, micropylar part of an adult ES, central nucleus short after the fusion of polar nuclei; 11, nuclei from the same ovule: one of a somatic cell and two pairs of nuclei from two binucleate ESs.

of seeds germinated. The attempts of controlled pollinations failed in about 200 pollinated flowers. Acetocarmine tests showed from 100 to 87 per cent unstained pollen in particular flowers.

Extremely poor seed-setting connected with very effective vegetative reproduction classifies *P. × mixta* as a vegetative apomict. However, agamospermy could also be expected according to the records of Forenbacher (1913) for *P. erecta* and Schwendener (1969) for *P. reptans*, *P. erecta* and *P. anglica*, for the putative parental species of *P. × mixta*. These three taxa are able to develop diplosporous and aposporous initial cells, and in *P. anglica* and *P. reptans* parthenogenesis was noted. So the genes for apomixis occur in the group, and the probability of agamospermy or at least of some elementary apomictic processes must be taken into consideration.

Some suggestions are expected from the progeny test. The plants were obtained after open pollination in the experimental field, the only technically possible way of getting more seeds from one plant (Table 1). The chromosome number of the pollen plant is of course speculative in each case. One cannot even tell if the plants are self-sterile or self-fertile on account of the difficulties in pollination of highly sterile individuals. The number of plants was low but they were cytologically differentiated; euploids and aneuploids occurred among them. The aneuploid numbers pointed to meiotic disturbances in *P. × mixta*, in the pollen plant or in both.

The plants from Rybnik, Silesia, and from Monks Wood, Huntingdonshire as well as from Wessington, Derbyshire (the last examined by Matfield *et al.* 1970) developed seeds, which germinated and their seedlings survived, after meiosis and fertilization as a rule. However, such chromosome numbers as 42, 56, 61, 63 and 93-7 suggested occasional formation of unreduced gametes. There is also a probability of some mechanisms which might occasionally raise the ploidy level of a plant. Nevertheless facultative apomixis in *P. × mixta* would be possible, but the supposition demands a confirmation of embryological facts.

The sterility of pollen in *P. × mixta* was connected with disturbances in meiosis: in diakinesis from 2 to 13 univalents occurred and occasionally one trivalent was formed. One to four chromosomes were left beyond equatorial plates in the I and II metaphases, laggards were visible in the I and II anaphase. As the result of these irregularities additional, small nuclei were formed in interkinesis and in the II telophase. Polyads had one to two microcytes and pollen degenerated after meiosis.

The most characteristic feature of the developmental processes in ovules of *P. × mixta* from the investigated populations were distur-

Table 1. Chromosome numbers in the progeny of P. × mixta (2n = 42) (open pollination in the experimental field)

Origin of maternal plants	Chromosome numbers										
	35	39	41	*42	44	49	50	*56	*61	*63	*93-7
Rybnik, Silesia	1	—	—	1	—	—	—	2	—	1	1
Monks Wood, Huntingdonshire	4	1	—	—	—	1	—	—	—	—	—
Wessington, Derbyshire (Matfield <i>et al.</i> 1970)	—	—	1	1	1	—	1	—	1	—	—

* Probability of unreduced ♀ gametes.

bances which contributed to the seed sterility of plants. In some flowers pistils and anthers degenerated at early stages, in others the sterility was connected with the retardation and irregularities of the development of the generative tissue. Both meiosis and the development of embryo sacs was affected. In addition, in many ovules dyad and tetrads degenerated or abnormal young embryo sacs occurred. The adult embryo sacs were rare in old ovules in relation to the small number of seeds collected from the plants.

At the beginning of flowering and anthesis uninucleate embryo sacs were visible in most ovules. It was a well-pronounced retardation also in comparison with *P. reptans*, whose ovules of comparable age contained eight- and seven-nucleate embryo sacs. In many flowers stigmas and styles dried before embryo sacs could reach maturity and be fertilized. Very often the ovaries with dry stigmas still contained uni-, bi- and four-nucleate embryo sacs or remnants of degenerated generative tissue.

Degeneration took place chiefly during meiotic stages and development of uni- and bi-nucleate embryo sacs. Before the degeneration as well as in ovules in which the developmental processes were more or less undisturbed, both diplosporous and aposporous initial cells and tetrads occurred. The origin of initial cells could be recognized only from the stage of meiosis until the stage of young uninucleate embryo sacs. (Figs. 1–6.)

Diplosporous initial cells prevailed. They belonged to the lateral or parietal archesporium. Enlarging of chalazal cells into aposporous initial was rarer. One to four young embryo sacs developed in one ovule. Unfortunately no mitosis in unreduced embryo sacs was found, but the nuclei in particular embryo sacs differed often in size. It was highly probable that these differences were connected with their reduced or unreduced state. As a rule one embryo sac only was successful. Parthenogenesis could not be demonstrated in the rarely occurring embryo sacs. (Figs. 7–11.)

In *P. × mixta* apomeiosis occurs in addition to meiosis. Parthenogenesis is difficult to prove either in embryological preparations or in experiment. Both tendencies, amphimictic and apomictic, are interrupted by strong sterility.

The stabilization of *P. × mixta* is achieved by vegetative reproduction. The occasionally formed viable seeds, thanks to their cytological differentiation, are the potential source of variability.

Speaking about significance of apomixis, one stresses often the possibility of stabilization of a hybrid, a new morphological form, by agamospermy. It is true, but on condition that the hybrid is fertile. Agamospermy itself is not an autonomic process beyond any control

of the developmental factors acting in the ovule. The genetic regulation of apomixis, simple or complicated, together with some external factors, influences the mode of reproduction. The realization of both amphimictic and apomictic processes requires similar fundamental conditions securing undisturbed development of viable seeds.

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THE *VERONICA HEDERIFOLIA* GROUP: TAXONOMY, ECOLOGY, AND PHYLOGENY

M. Fischer

ABSTRACT

1. The *Veronica hederifolia* group is a polyploid complex (the basic chromosome number being $x = 9$) of which up to now 5 taxa are known: *V. sibthorpioides* Deb., Deg. & Herv. ($2x?$), *V. stewartii* Pennell (= *V. hederoides* M. Fischer; $2x$), *V. triloba* (Opiz) Kerner ($2x$), *V. sublobata* M. Fischer (= *V. hederifolia* L. subsp. *lucorum* [Klett & Richter] D. Hartl; $4x$), and *V. hederifolia* L. s.str. ($6x$).

2. Detailed analysis showed that all of them – in spite of their great variability and modificability – are to be clearly distinguished morphologically from one another (Fig. 1) and that they are intersterile.

3. The ‘reliability’ (degree of variation) of all differential characters is judged, and the nature of the morphological limits between the taxa is discussed. Difficulties in identifying living individuals and herbarium specimens can be overcome by using a ‘collective index’ of the differential characters. As all the 5 taxa show different ecological positions and different areas as well, they doubtless merit specific rank.

4. Some characters display a clear correlation between variation and habitat (Fig. 2).

5. Geographical clinal variation within the microspecies is discussed, but requires further studies.

6. The allopolyploid origin of *V. hederifolia* L. s.str. (*V. triloba* \times *V. sublobata*) can be strongly assumed. A theoretical model of the phylogeny of the group is proposed (Fig. 3).

1. INTRODUCTION

1.1. The *Veronica hederifolia* group belongs to the large Section *Pocilla* Dumort. (= *Alsinebe* Griseb.) consisting of annuals mostly, some of them widely distributed on cultivated ground. This is also true for *V. hederifolia* s.l., and that is why every botanist knows my plant. It was known also for its great variability that seemed to defy any reasonable splitting. Some years ago (Fischer, 1967) the numbers of the chromosomes gave important hints for recognizing this ‘species’ as a species aggregate consisting of five distinct entities. As there are three

ploidy levels, these five taxa form a polyploid complex. There are three diploids, namely *V. triloba* (Opiz) Kerner, *V. stewartii* Pennell, and probably *V. sibthorpioides* Deb., Deg. & Herv. (the exact chromosome number is not yet known); one tetraploid: *V. sublobata* M. Fischer; and one hexaploid: *V. hederifolia* L. s.str. The basic chromosome number is $x = 9$. No aneuploid and no anorthoploid plants have been observed.*

1.2. The most closely related group is *V. cymbalaria* Bod. agg. which represents also a polyploid series ($2x$, $4x$, $6x$) of a few microspecies on $x = 9$ (Fischer, 1975).

1.3. Detailed studies, carried out over several years, on the variability of the three widespread taxa *V. triloba*, *V. sublobata* and *V. hederifolia* s.str. revealed distinct limits between them. The essential aim of this report is to show that it is important to know precisely the extent of variability of each differential character, that means their degree of 'reliability', because this is the prerequisite for the decision on the taxonomic treatment. I shall try to explain that these taxa merit specific rank: they are good species, no 'Linnean' ones of course, but – *sit venia verbo* – good microspecies.

2. THE DISTINGUISHING CHARACTERS OF THE FIVE SPECIES (SEE FIG. 1)

2.1. *V. sibthorpioides* Deb., Deg. & Herv. ($2x?$). Leaves thin, usually deeply 3-lobed, middle lobe longer than wide, obtuse-rounded. Pedicels not more than $1\frac{1}{2}$ times as long as the calyx, equally hairy on all sides. Calyx sparsely hairy, shortly ciliate. Corolla very small. Style c. 0.3–0.6 mm long. Fresh seeds unknown.

2.2. *V. stewartii* Pennell (= *V. hederoides* M. Fischer; $2n = 18 = 2x$). Leaves thin, bright green, very shallowly 3- to 7-lobed (i.e. crenate), middle lobe much wider than long, obtuse. Pedicels not more than $1\frac{1}{2}$ times as long as the calyx, equally hairy on all sides. Calyx glabrous or sparsely hairy, shortly ciliate. Corolla white, very small, not exceeding the calyx. Style c. 0.2–0.3 mm long. Seeds suborbicular, almost smooth (ribs indistinct), very pale, brim of the orifice smooth, shining.

2.3. *V. triloba* (Opiz) Kerner ($2n = 18 = 2x$). Leaves thick, dark green, deeply 3- to 5-lobed, middle lobe much wider than long, pointed. Pedicels not more than $2\frac{1}{2}$ times as long as calyx, usually glabrous

* Jongh & Kern (1973) report the number $2n = 28$ in '2 preparations' (out of 41), but they do not mention anything about the morphology of these plants. So I suppose that those plants very probably belong to quite a different species, e.g. *V. persica*.

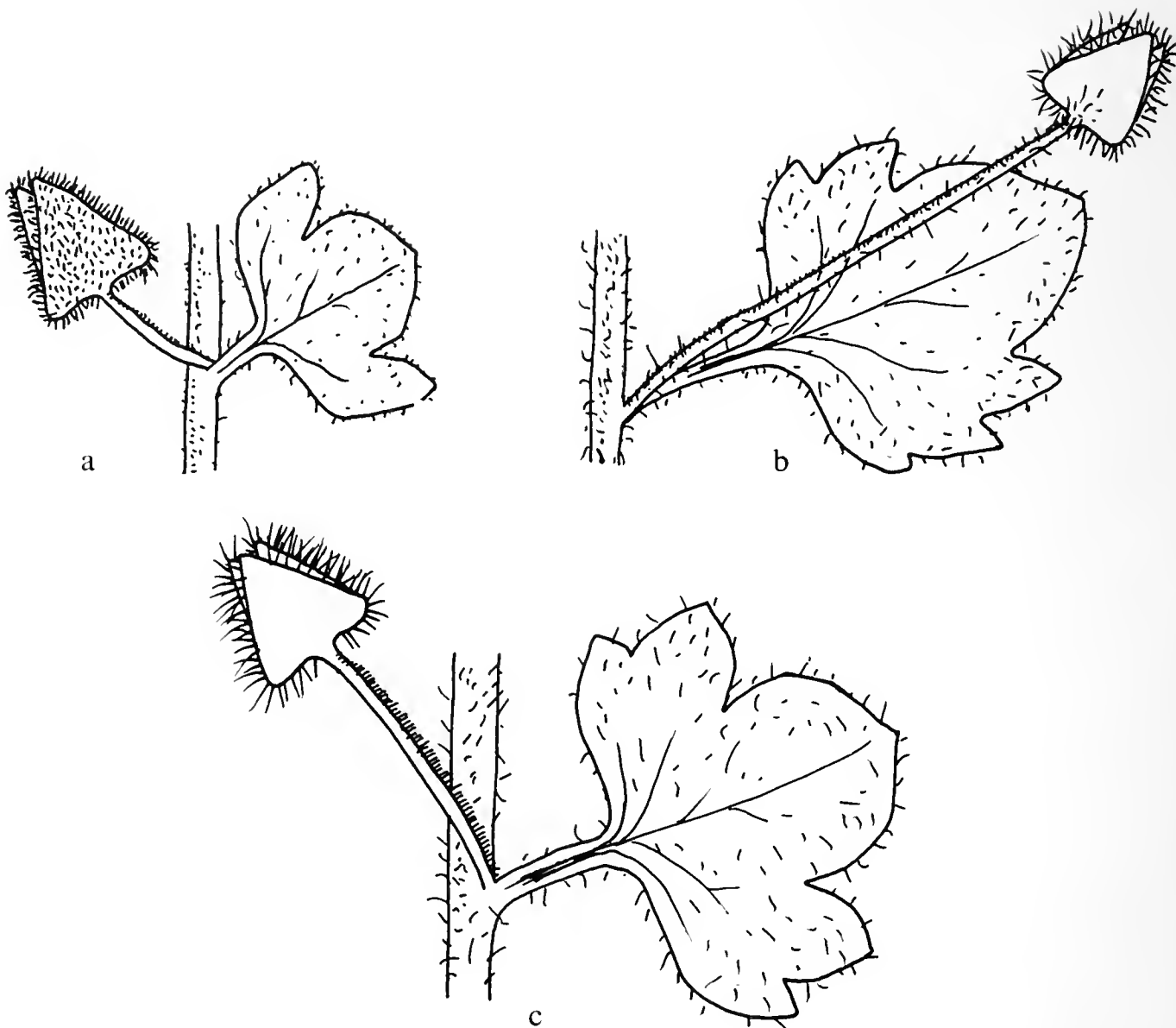


Fig. 1. Leaf, pedicel and calyx of: a, *V. triloba*; b, *V. sublobata*; c, *V. hederifolia* s.str.

except for an adaxial row of short hairs. Calyx pubescent, shortly ciliate. Corolla small, dark blue. Style c. 1 mm long. Seeds oblong, distinctly ribbed, brownish, brim of the orifice with distinct ridges too.

2.4. *V. sublobata* M. Fischer (= *V. hederifolia* L. subsp. *lucorum* [Klett & Richter] D. Hartl*; $2n = 36 = 4x$). Leaves thin, relatively bright green, rather shallowly 5- to 7-lobed, middle lobe as long as wide or slightly longer than wide, \pm pointed. Pedicels $3\frac{1}{2}$ –7 times as long as calyx, with an adaxial row of short hairs and usually some patent hairs outside this row, especially in distal half. Calyx glabrous or very sparsely pubescent, shortly ciliate, cilia a little longer than in *V. triloba*. Corolla small, pale lilac. Style usually not more than 0.5 mm long. Seeds suborbicular, shallowly ribbed, somewhat red-brown, brim of the orifice distinctly smooth and shining, whitish.

2.5. *V. hederifolia* L. s.str. ($2n = 54 = 6x$). Leaves somewhat thick, rather dark green (intermediate between *V. sublobata* and *V. triloba*),

* There is an unfortunate misprint in the index to *Flora Europaea*, 3: 370. Correctly it should read there: *sublobata* M. Fischer, 250 (57c), not (57b).

3- to 5-lobed, middle lobe wider than long, pointed, incisions distinctly deeper than in *V. sublobata*, especially in upper leaves. Pedicels (2–)3–4 times as long as calyx, usually glabrous except for an adaxial row of patent hairs (which are longer than in *V. sublobata*). Calyx glabrous except for rather long, patent cilia. Corolla relatively large, bright blue with white centre. Anthers large and conspicuously blue. Style 0.7–1 mm long. Seeds large, broadly oblong to orbicular, ribbed, pale yellowish, brim of the orifice broad, partly without ridges, somewhat shining.

2.6. Annotation. More detailed descriptions (e.g. on the size of leaves, petioles, corollas, anthers, seeds, pollen grains and stomata) are given in Fischer (1967) and in Hartl (1968; in *V. sublobata* erroneously the description of length of pedicels is omitted).

3. TAXONOMIC EVALUATION, VARIATION OF CHARACTERS; NATURE OF THE LIMITS BETWEEN THE THREE WIDESPREAD SPECIES *V. triloba*, *V. hederifolia* S.STR., AND *V. sublobata*

3.1. The differences between the 5 taxa are approximately equal, so all have to be treated as of equal rank.

3.2. The distinguishing characters show a different amount of variation. I arrange them in a series from 'rather constant' (little variation) to 'rather variable' (\pm overlapping).

(a) Colour of corolla. Unexpectedly a very good character in the living plant, remarkably useful for quick and easy identification in the field.

(b) Shape, colour, surface and orifice of the mature and fresh seeds. After c. 2–3 years, however, the seeds become strongly rugulose and dark, and finally black, so the important characters vanish.

(c) The shape of the upper leaves provides a very good character in spite of its large variability, but it is not easy to describe it, and it needs some training to recognize its value. Important are the degree of incision, the shape of the middle lobe, the number of lateral lobes, and particularly the combination of these features. It is necessary also to consider the changes along the stem (lower leaves to upper leaves) and the relation to the absolute size of the plant.

(d) Indumentum of calyx (length of cilia).

(e) Length of style.

(f) Succulence and colour of the leaves.

(g) Indumentum of pedicels. On an average, about one-third of the individuals in *V. sublobata* have no hairs besides the row, but the hairs of the row are usually shorter than in *V. hederifolia* s.str. Unfortunately in Fischer (1967) too little emphasis was laid on the variation of this

character (mainly genetically caused, but in *V. hederifolia* s.str. sometimes a damp habitat seems to induce hairs outside the row); it is implied in the scatter diagram but was erroneously omitted in the description, and so it is not mentioned by Hartl (1968) nor by Hess, Landolt & Hirzel (1972).

(*h*) Average length of pedicels. This character is rather variable.

The characters (*a*) and (*b*) show almost no overlapping at all; (*c*), (*d*), (*e*) show some small extent of overlapping between the taxa; (*c*), (*f*), (*g*) and (*h*) are modifiable by ecological conditions of the habitat (see section 4). Apart from that, most of the variation obviously has a genetic background. Variation in chromosome number is not known (see section 1.1).

3.3. For the identification of specimens of the *V. hederifolia* group careful consideration of all or most of the above-mentioned characters and of their variability is necessary, and it is also useful to know the habitat (see section 4.2). Despite the usual lack of fresh mature seeds and of detailed information on the colour of the flower, c. 75 per cent of herbarium material can be identified, given some experience. A collective index that considers the different reliability of the characters can be useful for determination: the variation of each character represents a more or less continuous series. Value 1 is co-ordinated to the average state of each character in *V. triloba*, value 3 to *V. hederifolia* s.str., value 5 to *V. sublobata*. The 'weighting' of the characters is managed by using different coefficients for some characters (e.g. coefficient 3 for the highly reliable characters (*a*), (*b*), (*c*); coefficient 2 for the slightly less reliable characters (*d*) and (*e*); and coefficient 1 for the remaining characters). By summing the values for each character, a collective index for a given specimen is calculated: Thus the average *V. triloba* obtains index 16 (or $16/16 = 1$), the average *V. hederifolia* s.str. obtains index 48 (or $48/16 = 3$) and the average *V. sublobata* obtains index 80 (or $80/16 = 5$). By this method the existence of 'gaps' marking distinct limits between the taxa can be shown.

3.4. I shall now sum up all the evidence for attributing specific rank to the taxa within *V. hederifolia* group. By careful examination of thousands of specimens and taking into account the above-mentioned considerations on the different variational amplitude of the characters, only very few individuals could not be assigned to one of the three taxa. This is evidence for strong genetic barriers and corresponds to the breeding system in this group which is characterized by autogamy (inbreeding) and strict dissimilarity in ploidy level. True morphological intermediates and aberrants are very rare, and may be the result of some very restricted gene-flow (casual hybridization). The taxa also behave differently ecologically as well as geographically, although occurring

sympatrically in large regions and growing together in some habitats (see sections 4 and 5).

3.5. Recently the *V. hederifolia* group has been studied in some north-western and northern European countries, namely in the Netherlands (Jongh, 1968; Jongh & Kern, 1971; Jongh & Kern, 1973); in Sweden (Nordenstam & Nilsson, 1969); in Finland (Saarisalo, 1971); and in Denmark (Pedersen, 1972). These authors recognized two strains (*V. triloba* is lacking in these regions) and they found the same correlations of characters. But Nordenstam & Nilsson (1969) and Jongh & Kern (1971) are not convinced of the existence of distinct gaps, they claim to have observed many intermediate forms, and so they prefer to treat the strains as subspecies (*V. hederifolia* subsp. *hederifolia* and subsp. *lucorum*; the same conception has been adopted by Saarisalo (1971), Pedersen (1972), and Walters & Webb (1972)). Unfortunately, however, the salient question of limits within the striking variation of several characters was not regarded carefully enough. Nordenstam & Nilsson's 'intermediate' type C is clearly *V. sublobata* (this seems to be also the opinion of Pedersen), the other 'intermediate' type B probably is an aberrant population (occurring in Uppsala only?) of *V. hederifolia* s.str. The length of pedicels and the important seed characters obviously have been neglected. I doubt the three different chromosome numbers in the offspring of type A (= *V. sublobata*) on methodical grounds (examinations of seedlings only!). Saarisalo (1971) and Pedersen (1972) do not report any difficulties with intermediate specimens. According to specimens of the herbaria W, WU (Vienna), CGE (Cambridge), E (Edinburgh), K (Kew), and LD (Lund) and through personal communications by British field botanists I conclude that in Great Britain (as in Scandinavia and in the Netherlands) the structure of the group is essentially the same as in Central Europe, i.e. that *V. sublobata* and *V. hederifolia* s.str. fit better into the concept of microspecies rather than of subspecies.* A thorough study, however, and a detailed knowledge, is inevitable to disclose the morphological and genetical limits of the taxa which are concealed by an intricate pattern of variation of the different characters. My present report wishes to draw attention to the peculiar problems of revealing the very nature of microspecies within a complicated aggregate like the *V. hederifolia* group.

3.6. A satisfactory analysis was accomplished by Benoit (1971) who confirms the distinctness of *V. hederifolia* and *V. sublobata* in Wales and who tried to hybridize the species, but did not succeed: this he interprets as further evidence for genetic distinctness.

* For interesting discussions and help I am particularly indebted to Dr S. M. Walters (Cambridge), Mr P. D. Sell (Cambridge), Mr E. L. Swann (King's Lynn), Mr R. P. Libbey (King's Lynn), and Mrs C. Dony (Luton).

3.7. Annotation to the drawings in Hess, Landolt & Hirzel (1972) who treat *V. triloba*, *V. hederifolia* s.str. and *V. sublobata* as species: the cuneate leaf of '*V. triloba*' is very untypical, and the leaves of '*V. hederifolia*' are typical leaves of *V. sublobata*.

4. VARIATION DEPENDENT ON THE HABITAT (SEE FIG. 2)

4.1. The ecological positions of the 3 widespread species. In the diagram Fig. 2 the horizontal ordinate represents an ecological gradient from shady/damp/eutrophic to sunny/dry/less eutrophic. The frequency (vertical ordinate) of the three species in the different habitats is shown by graphs in the lower half of the diagram: shady/damp habitats are typical for *V. sublobata*, but it extends in small number into warm/dry habitats too; *V. hederifolia* s.str. has its maximum in arable land and is missing in damp woodland (in Central Europe; it grows in mountain forests of Southern Europe, where there is no *V. sublobata*). This distribution of ecological preferences of these two species is confirmed by all recent North European authors dealing with our subject. *V. triloba* extends from warm/dry steppe-like habitats to arable land (in warm regions of Central Europe and in the Mediterranean). In arable land of, for example, south-eastern Central Europe all 3 species can grow together.

4.2. Some of the differential characters (namely shape, succulence and colour of the leaves, length and – in a low degree – indumentum of the pedicels) are strikingly liable to modification to a certain extent. This is mentioned already in Fischer (1967: 204) and it is confirmed by Nordenstam & Nilsson (1969: 235) but wrongly interpreted. This fact was one of the main reasons for difficulties in subdividing *V. hederifolia* agg. in former times and is responsible nowadays for the troubles and doubts of some contemporary authors. As these characters are conspicuous and important for the habit of the plant it is useful for recognition in the field to know about this. The remaining part of the diagram (Fig. 2) shows the range of variation of the above-mentioned characters in the three species as depending on the ecological position. The horizontal ordinate is the same as in 4.1; the vertical ordinate, however, here means the state of those modifiable characters, ranging from extreme '*sublobata*-like' (value 6 according to section 3.3) to extreme '*triloba*-like' (value 0). Position and size of the areas of each species symbolize the range of variation (modification and genetically caused variation). In the typical '*sublobata*-habitat' *V. sublobata* looks typical. In an intermediate habitat, however, the plants become somewhat similar to *V. hederifolia* s.str., and in a '*triloba*-habitat' the leaves and pedicels look even similar to *V. triloba*. But in this dry, warm, steppe-like place

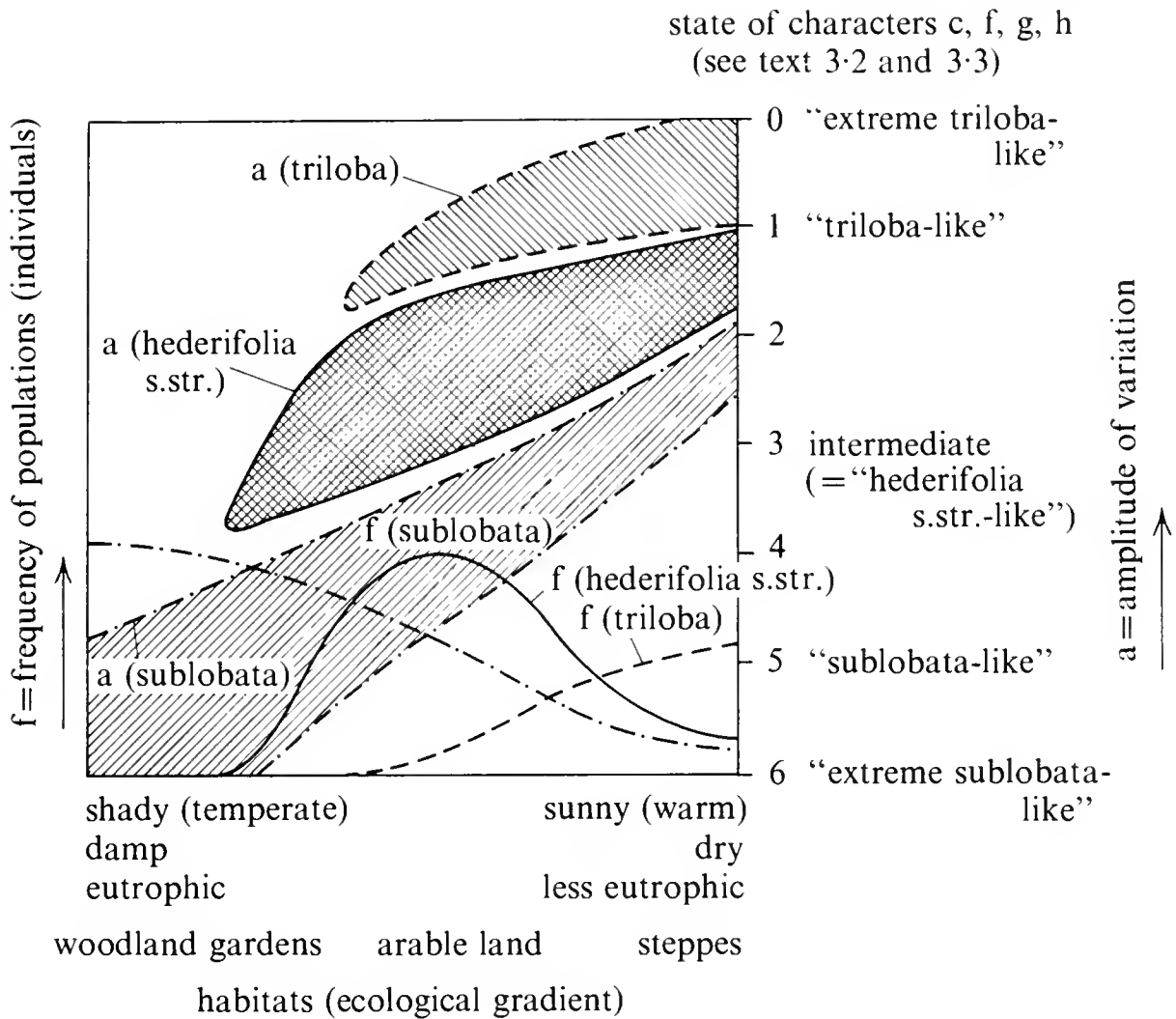


Fig. 2. Frequency and variability of the 3 main species of the *Veronica hederifolia* group in different habitats.

there is still an appreciable difference from true *V. triloba*, because this looks even more 'extreme'. *V. hederifolia* s.str., in a rather damp and eutrophic position, gets some features of *V. sublobata* in its leaves and pedicels, but it still remains very easily distinguishable because *V. sublobata* in the same spot looks much more 'typical *sublobata*-like'. Similarly, *V. triloba* in comparatively damp habitats may slightly approach *V. hederifolia*, but here *V. hederifolia* has got some resemblance to *V. sublobata*, and thus the relative morphological distance remains approximately the same. Notice that there is no overlapping at all within a given habitat because the three species are modifying their characters (more precisely: the range of variation of their characters) in a 'parallel way'! Determining herbarium specimens without any knowledge of the habitat, however, means concentrating on other characters which, nevertheless, will allow correct identification.

4.3. In the very accurate study of Saaristo (1971) variation in *V. sublobata* (which he calls *V. hederifolia* subsp. *lucorum*) in Finland is discussed on the basis of herbarium material. The 'rye-field type' perhaps represents only an extreme modification of dry habitats. The 'weedy type' is the usual modification of open habitats and common also in Central Europe.

5. GEOGRAPHICAL VARIATION

There is some geographical variation within each of the three widespread species which has not yet been adequately studied. *V. triloba* is obviously more variable in the eastern part of its area (Greece and Asia Minor), which seems to be the centre of origin. My own quite recent field observations (unpublished) on the island of Cephalonia (Ionian Islands, Greece) showed that even here, *V. triloba* and *V. hederifolia* s.str., growing together in cereal fields, could be easily distinguished. *V. triloba* was described from the south-eastern part of Central Europe, but is probably spread throughout the whole Mediterranean as a weed (Fischer, 1974), only it has been overlooked or not separated from *V. hederifolia* s.str.

V. sublobata is widely distributed in Central, Eastern, Northern and North-western Europe. I have not been able to recognize any clear cline, although the populations of, say, England and Central Europe show some characteristic differences, which lie within the range of variation described above. The relative ecological positions of the microspecies in England as well, seem in general to be the same as on the Continent and in Northern Europe, but further information about this is required.

In *V. hederifolia* s.str., which occupies the largest area, embracing the areas of all the other microspecies, the situation is similar to that of *V. sublobata*. Thus only in south-eastern Central Europe and in the northern part of the Balkan peninsula are those 3 species sympatric. It is not yet quite clear if there are critical true intermediates in this region.

The distribution and relative frequency within the British Isles seems to be interesting: in South-eastern England, with its relatively continental climate, *V. sublobata* seems to dominate, whereas in Scotland apparently *V. hederifolia* s.str. is the commonest species. I hope that more detailed information will soon be available.

V. sibthorpioides and *V. stewartii* have rather restricted areas in the mountains of the South-western Mediterranean and in the Himalaya respectively.

6. PHYLOGENY (SEE FIG. 3)

6.1. The hexaploid species *V. hederifolia* s.str. obviously originated by allopolyploidy. Its parents are *V. triloba* (diploid) and *V. sublobata* (tetraploid). There is a lot of good evidence for this hypothesis, as follows. Most of the characters of *V. hederifolia* s.str. are clearly intermediate: (1) shape, succulence and colour of leaves, (2) length of pedicels, (3) colour of the corolla, (4) shape of seeds. Also the range

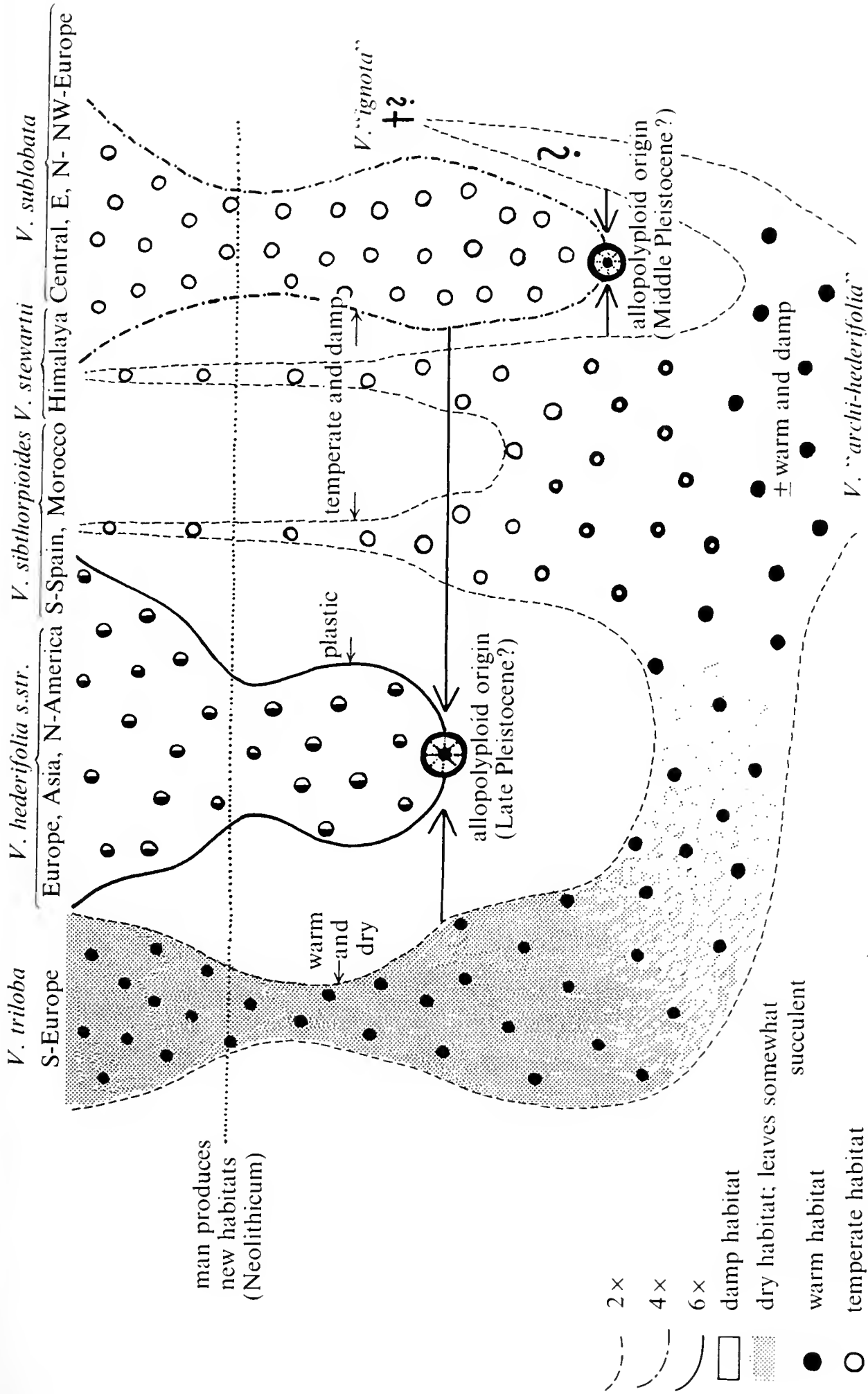


Fig. 3. Phylogeny of *Veronica hederifolia* agg. with indication of ploidy-levels, habitats, geographical distribution and size of areas.

of variation fits exactly between those two parents, and the intermediate autecology provides further evidence. Two characters of *V. hederifolia* s.str. are common to one parent: the length of style and the indumentum of pedicels. One character is new: the surface of the sepals is glabrous. Three size-characters are correlated with the ploidy level: length of cilia of sepals, size of corolla, and average size of seeds.

No attempts so far have been made to synthesize artificially the allohexaploid. I do not consider this experiment to be very urgent because I think my hypothesis is at any rate well supported. Furthermore, *V. hederifolia* s.str. did not arise very recently and therefore may have undergone already some evolutionary changes.

6.2. The relationships between the other members of the group are not as evident. But, in combination with some general considerations, it is possible to draw an outline of the evolution in this species aggregate.

V. sibthorpioides and *V. stewartii* are rather closely related taxa; their diploid (or presumably diploid) chromosome numbers and their small, restricted, disjunct areas may indicate their great age and their relic position. Both the Himalaya and the calcareous mountains of Southern Spain and Morocco are 'conservative' regions with several other regressive and ancient endemics.

6.3. The descent of *V. sublobata* is uncertain. Presumably *V. sublobata* originated by allopolyploidy too, an earlier parallel case which happened perhaps during the Middle Pleistocene. One of its ancestors probably is *V. stewartii* because of some characters in common. The other ancestor which contributed the long pedicels probably became extinct (*V. 'ignota'*).

6.4. Now I would like to propose some reflections on the possible evolutionary history of our group. Let us assume that the ancestors of the group were growing in rather damp and warm Early Pleistocene forests at the beginning of seasonal rhythm. The myrmecochory of the group (and of several other members of Section *Pocilla*) may be considered as a characteristic feature of a woodland plant.* Moreover, most of the life cycle is accomplished in (early) spring time: vegetative development, flowering and seed-setting takes place within a few weeks between March and May because of sufficient light supply in a broad-leaved deciduous forest in this season only. This quality of the life cycle proved to be an important determinant for the future spread into cultivated land.

The dating of the evolutionary steps is difficult and very hypothetical of course. Because of the three ploidy levels we must suppose that the

* The seeds bear elaiosomes.

group differentiated already much earlier than in postglacial times. As there are three diploid species still existing, however, the group's age cannot be very great.

Initially, considerable divergent evolution took place at the diploid level: *V. triloba* arose by adaptation toward resistance to drier conditions in the course of the gradual increasing of dry habitats during the Early Pleistocene. Its leaves became fleshy and deeply lobed. On the other side, together with the arising of mountains, some strains of 'archi-*hederifolia*' had to answer the challenge of climatic changes towards cooler, temperate conditions. In this way in different mountain areas *V. sibthorpioides*, *V. stewartii* and *V. 'ignota'* originated. Apparently they have not been very successful, but one might consider that these mountainous species were subject to large geological changes in their areas and habitats, typical circumstances favouring allopolyploidy. Indeed, an allotetraploid offspring of those mountain species, namely *V. sublobata*, managed to spread more successfully.

6.5. Fortunately we know more about the second and more recent event of allopolyploidization: the origin of the hexaploid *V. hederifolia* s.str. probably occurred during the Later Pleistocene. We have to imagine that the warm and dry habitats were occupied by *V. triloba*, whereas the temperate and damp woodland localities had been colonized by *V. sublobata*. There may also have been some areas without either of these species. In the course of climatic changes and migrations of the flora there was an opportunity for both species to come into close contact. I think, however, that the most important prerequisite for the origin of a high allopolyploid was the presence of a vacant ecological niche, some ecological vacuum, causing a selective pressure towards the evolution of a new *hederifolia*-strain which would fit into the newly established forest habitats in interglacial and postglacial times. *V. triloba* on the one hand was too strictly xerothermic and could not manage to grow in a shady forest. On the other hand, *V. sublobata* was not able to grow under dry conditions. That was the reason why a hybrid between these species could best succeed in filling that niche. It combines genes for dry and warm with genes for damp and temperate habitats. The genetic barrier between the parents was overcome by polyploidy. Evolution by simple divergent gene-differentiation has proved not to be sufficient to conquer those new habitats within the short time at its disposal. So reticulate evolution by allopolyploidy was the appropriate means to produce an aggressive new species which could provide survival and expansion of the group. It may have expanded even at the expense of *V. triloba* and *V. sublobata*. *V. hederifolia* s.str., because of its 'rich' heritage, proved to be extremely plastic, and so it was much favoured later on when new, artificial habitats

were produced by man from Neolithic times. It became one of the most successful weeds, accompanying man in his cultivated land as an archaeophyte. To a lesser extent, *V. sublobata* also succeeded in becoming a synanthropic plant, but it still prefers woodland. Even the diploid *V. triloba* could by anthropochory enlarge its area to a certain degree, but it is less plastic and restricted to warm countries.

It is of interest to find *V. hederifolia* s.str. growing in deciduous mountain forests in the central part of the Mediterranean, e.g. in Sardinia (Monte Gennargentu), in Northern Sicily (Monti Nebrodi), and in central Italy (Monte Garganico). Probably these are original, autochthonous habitats of the species. These regions have been geologically rather unstable, and have suffered great changes; no diploid, old ancestor could survive here, and perhaps it was here, where the young hexaploid *V. hederifolia* s.str. originated.

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CARYOSYSTEMATIC STUDY OF SOME SPECIES OF THE GENUS *CENTAUREA* L. IN THE WESTERN MEDITERRANEAN BASIN

M. J. Fernandez-Morales and C. Gardou

ABSTRACT

This report gives the chromosome numbers of 24 populations belonging to three sections of the genus *Centaurea* L.

In the section *Acrocentron* Cass. we studied *C. granatensis* Boiss., *C. ornata* Willd. var. *microcephala* Wk. and var. *macrocephala* Wk., and *C. saxicola* Lag. In the section *Cyanus* Cass. we studied *C. variegata* Lmk., and in the section *Seridia* Juss. we studied *C. aspera* L. ssp. *stenophylla* Wk. and ssp. *subinermis* DC.

Several species with restricted areas of distribution are studied for the first time; other results agree with previous reports dealing with plant species from other areas. We found that supernumerary chromosomes and irregular meiosis with reciprocal translocations between non-homologous chromosomes were frequent. They perhaps explain the multitude of taxa described in the genus *Centaurea* L.

Les auteurs ont effectué la caryologie de 24 populations appartenant à trois sections du genre *Centaurea* L.

Dans la section *Acrocentron* Cass. nous avons étudié *C. granatensis* Boiss., *C. ornata* Willd. var. *microcephala* Wk. et var. *macrocephala* Wk., *C. saxicola* Lag. Nous avons aussi étudié, dans la section *Cyanus* Cass., *C. variegata* Lmk. et, dans la section *Seridia* Juss., *C. aspera* L. ssp. *stenophylla* Wk. et ssp. *subinermis* DC.

Plusieurs nombres chromosomiques nouveaux, relatifs à quelques taxons à aire géographique restreinte, sont rapportés. Les autres résultats complètent, pour d'autres localités, des nombres chromosomiques déjà connus. Nous avons remarqué que les chromosomes surnuméraires et les méioses irrégulières, avec des translocations hétérozygotes réciproques et des phénomènes de caténation, étaient fréquents. Ils expliquent peut-être la multitude de taxons décrits dans le genre *Centaurea* L.

INTRODUCTION

The genus *Centaurea* L. was divided by Hoffmann (1897) into 41 sections. Most of them contain several endemic Mediterranean species. In this paper we study karyologically 24 populations of *Centaurea* L. belonging to three sections: *Cyanus* Cass., *Acrocentron* Cass. and *Seridia* Juss. The authors worked simultaneously at Orsay and at Malaga and they grouped their results in this paper.

Most of the plants are perennial herbs, from natural habitats in south France, Spain and Morocco, and are cultivated in the Orsay experimental garden. The determination of the chromosome numbers was based chiefly on the study of root-tip mitosis and the analysis of chromosome pairing in bud-flower meiosis. Size and shape chromosome comparisons were made according to the method of Essad (1962-6).

RESULTS

Section *Acrocentron* Cass.

In this section we studied three Spanish endemic species: *C. ornata* Willd., *C. granatensis* Boiss. and *C. saxicola* Lag. The first one is widely represented in the whole of the Iberian peninsula and the two others have restricted areas of distribution in south-east Spain.

(1) *Centaurea granatensis* Boiss.

This species of the high calcareous mountains in the south-east of Spain is typically found in the communities of pungent xerophytes belonging to the *Erinacetalia* Quezel 1951.

We studied *C. granatensis* Boiss. in the following regions:

1455: Sierra Nevada, province of Granada, Los Aloyos de Dilar about 2,100 m altitude, calcareous rocks; $2n = 20$. 1456: Sierra Nevada, province of Granada, pass between the Dornajo and the Penones of San Francisco, calcareous rocks about 2,000 m altitude; $2n = 20$ (Fig. 17). Gr.: Sierra de la Yedra (Sierra de Alfacar), province of Granada, calcareous soil about 1,400 m. altitude; $2n = 20$ and $n = 10$ (Figs. 6 and 7).

In mitosis we observed $2n = 20$ chromosomes in the three populations studied. For the section *Acrocentron* Cass. the basic chromosome number is $x = 10$: *Centaurea granatensis* Boiss. must then be considered as a diploid. We carried out karyograms of the three populations according to the method of Essad (1962). Amongst the 10 pairs of chromosomes, 6 are formed by heterobrachial chromosomes, 2 of which have satellites, and 4 by isobrachial chromosomes (Fig. 5 and



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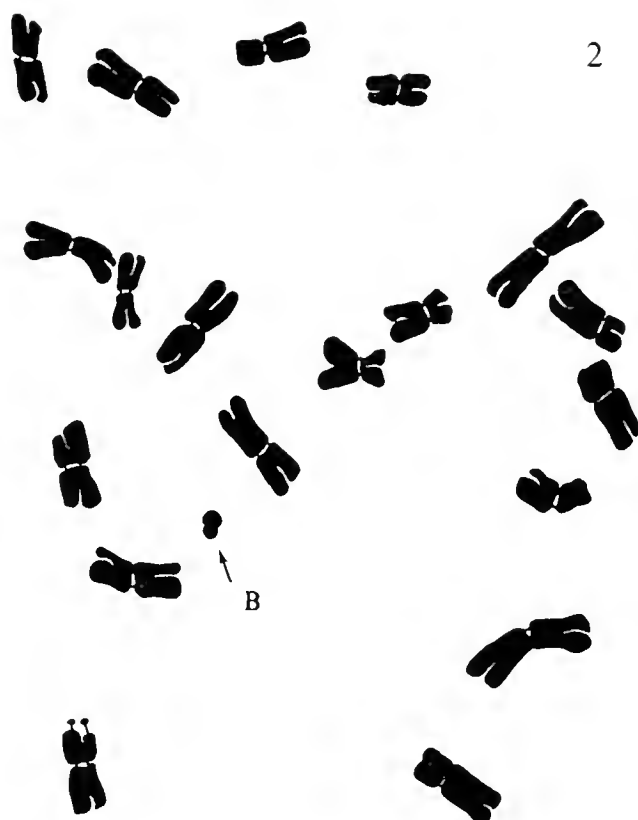


Fig. 1. Somatic chromosomes of *C. ornata* Willd. var. *microcephala* Wk., population 1289, $2n = 20$.

Fig. 2. Somatic chromosomes of *C. ornata* Willd. var. *microcephala* Wk., population 1336, $2n = 20 + 1B$.

Fig. 3. Somatic chromosomes of *C. variegata* Lmk., population 1236, $2n = 40$.

Fig. 4. Somatic chromosomes of *C. variegata* Lmk., population 1293, $2n = 20$.

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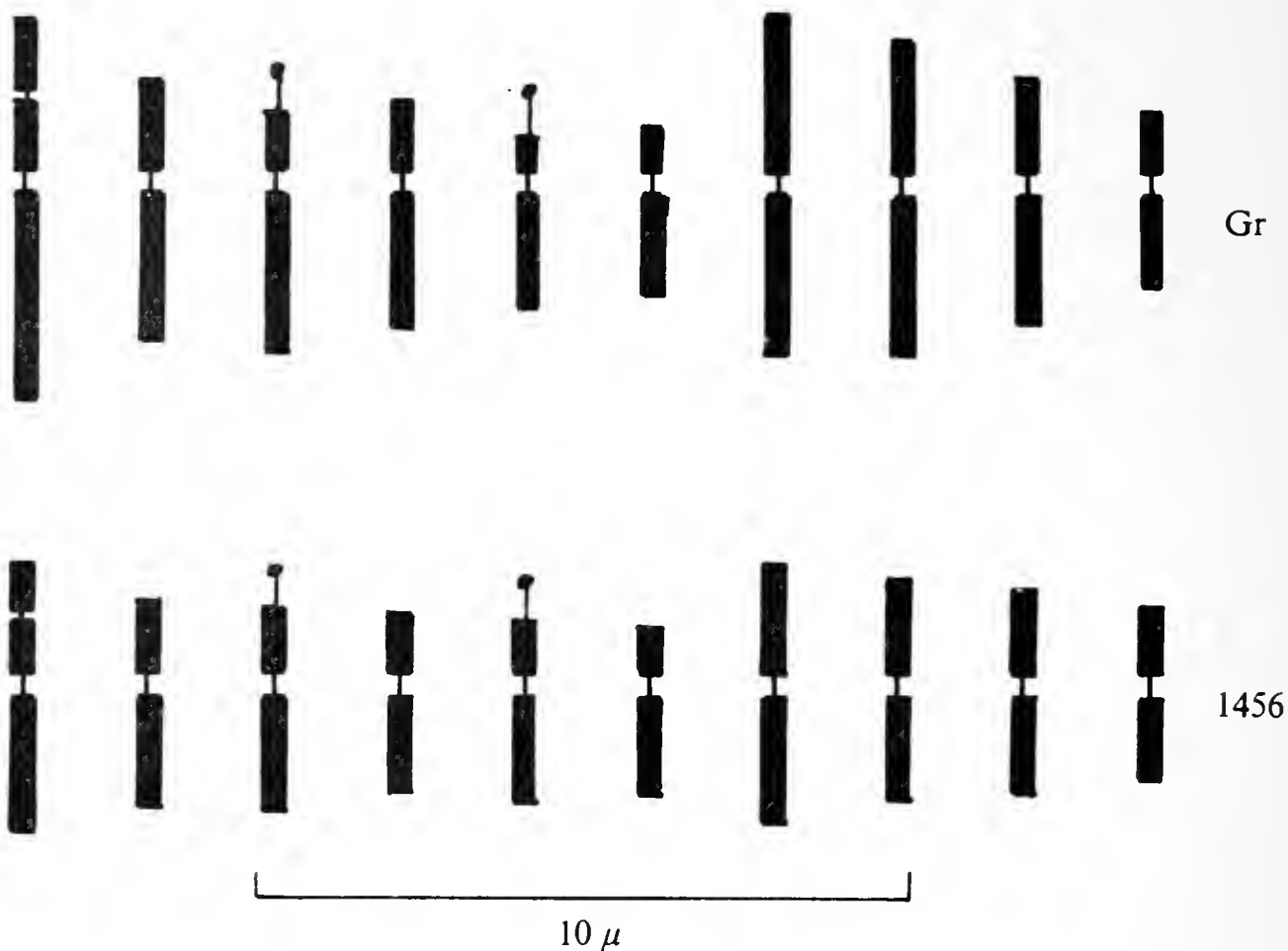


Fig. 5. Karyotypes of two populations of *C. granatensis* Boiss., Gr. Alfacar and 1456 Dornajo.

Table 1). Furthermore, the biggest heterobrachial chromosome bears secondary constrictions on one of the arms: this can be seen on Fig. 5.

We studied the meiosis of this species in the population Gr. of the Sierra de Alfacar. In some cells the chromosomes are paired in diakinesis and in metaphase I forming 10 bivalents normally. In other cells chromosome pairing is irregular: besides some bivalents there are a certain number of univalents (Fig. 7) or chromosome associations tending to form tri-, quadri- or quinquevalents (Fig. 6) or zigzag chains showing reciprocal translocations like the well-known ones of the genus *Oenothera* L. or *Campanula* (Tourn.) L. The chromosome segregation in anaphase I is somewhat irregular, with the formation of chromatid bridges. Finally the pollen of this plant population contains 50 per cent of abnormal cells and is partly sterile. In comparison we observed the pollen of two other populations previously studied in mitosis. The pollen is normal in the Aloyos population (1455) and it contains 43 per cent of abnormal small round grains in the Dornajo population (1456).

These observations of meiosis and pollen show that there is a slight genetic imbalance in *Centaurea granatensis* Boiss., which is probably due to hybridization between populations already partly genetically

Table 1. *Characteristic size proportions of the ten chromosomes in Centaurea granatensis Boiss.*

Refer- ence number	Locality	Heterobrachial chromosomes					Isobrachial chromosomes				
		1	2	3	4	5	6	7	8	9	10
Gr	Alfacar	c/l T _m	0.71 1.25	0.60 1.05	0.36 0.98	0.55 0.92	0.34 0.66	0.43 0.66	0.82 1.32	0.75 0.99	0.83 0.72
1456	Dornajo	c/l T _m	0.73 1.29	0.59 0.99	0.55 0.99	0.63 0.87	0.50 0.85	0.45 0.79	0.81 1.08	0.93 0.99	0.87 0.83

T_m, proportion of the total length of each chromosome to the mean length of the whole metaphase plate chromosome.
c/l, proportion for each chromosome of short to long arms. When c/l is lower than 0.75 there is a heterobrachial chromosome, and when c/l is equal to or greater than 0.75 there is an isobrachial chromosome.
These proportions represent the mean of thirty metaphase plate measurements.
Chromosomes with satellites are enclosed in a box.

isolated. However, there is no morphological characteristic enabling us to distinguish these populations from each other.

(2) *Centaurea ornata* Willd.

This taxon is very polymorphous. Willkomm (1870) already suspected the existence of this polymorphism and created two varieties, *macrocephala* Wk. with big capitulum, and *microcephala* Wk. with little capitulum.

As a result of this polymorphism, this species can be found in numerous plant communities in the whole Iberian peninsula, belonging to the *Rosmarinetalia* Br.-Bl. (1931) 1952, to the *Thero-Brachypodietalia* Br.-Bl. (1931) 1936 or to the *Ulicino-Cistetalia* Br.-Bl., Pinto da Silva and Roseira 1964.

We studied the karyology of this taxon from 9 areas in central and south-eastern Spain (Fig. 11) as follows:

1286: San Rafael, province of Segovia, Sierra of Guadarrama, granitic soil about 1400 m altitude; $2n = 40$. 1289: Valdemoro, province of Madrid, in the lower part of the gypseous hills, 600 m altitude; $2n = 20$ (Fig. 1). 1295: Los Molinos, province of Madrid, Sierra de Guadarrama, sandy granitic soil, 1400 m altitude; $2n = 40$ (Fig. 14), Gardou (1972). 1306: Gabaldón, province of Cuenca, calcareous red marls; $2n = 20$. 1336: Pass of Despeñaperros, province of Jaen, about 1100 m altitude; $2n = 20+0-1$ B (Fig. 2). 1337: Tembleque, province of Toledo, in the lower part of the gypseous hills; $2n = 40+0-5$ B (Fig. 13). 1340: Codos, province of Zaragoza, Sierra de Espigar, 1300 m altitude; $2n = 40$. Mo.: Sierra de la Yedra (Sierra de Alfacar), province of Granada, along the path in calcareous soil about 1400 m altitude; $n = 10$ (Figs. 8, 9 and 10). K.: Sierra Nevada, province of Granada, central path of Diechar, calcareous soil about 1400 m altitude; $2n = 20$ (Fig. 12).

We noticed that the smallest-flowered populations (1289, 1306, 1336, Mo. and K.), that is those belonging to the var. *microcephala* Wk. are diploids: we counted $2n = 20$ chromosomes in 1289, 1306, 1336 and K. and $n = 10$ for the Mo. population. We also carried out idiograms on the four diploid populations studied in mitosis. These four populations have different idiograms (Table 2): out of the 10 chromosome pairs there are, according to the different populations, from 3 to 6 isobrachial chromosome pairs; there are also one or two chromosome satellite pairs. Furthermore in some plants of the Despeñaperros population (1336) we observed a supernumerary chromosome (Fig. 2). These observations indicate a different origin or a different evolution for each of these populations.

The four other populations can be divided into two groups:

(a) Populations with medium-sized flowers 1286 and 1295. They have $2n = 40$ chromosomes amongst which 4 are satellite-bearing (Fig. 14),

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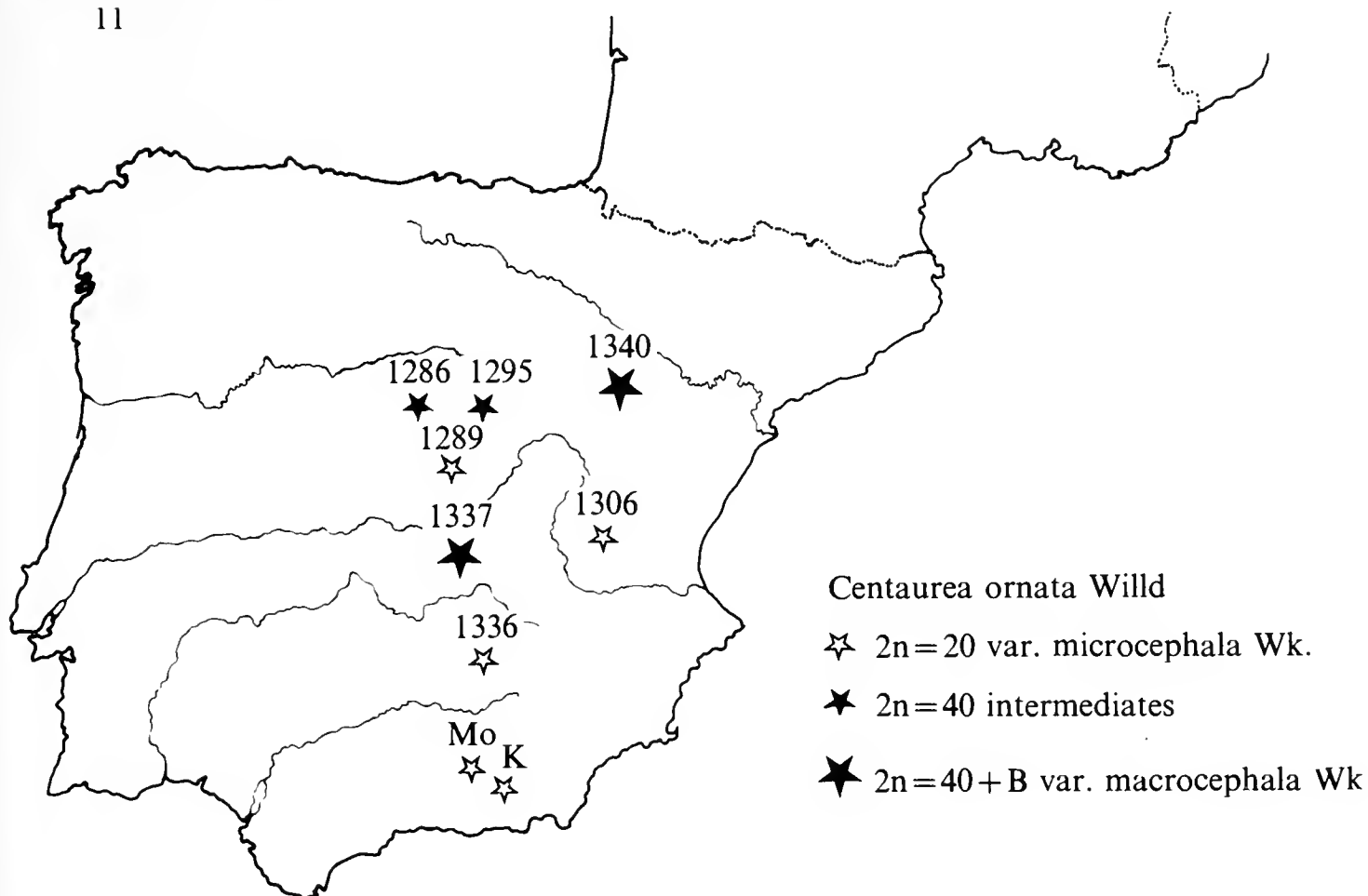


Fig. 11. Geographical distribution of the nine populations karyologically studied in *C. ornata* Willd.

as is the case of the diploid var. *microcephala* Wk. These two populations grow on the granitic soil of the Guadarrama Sierra.

(b) Populations with very big flowers 1337 and 1340 belonging to the var. *macrocephala* Wk. They have $2n = 40$ with from 0 to 5 supernumerary chromosomes according to the individual plants (Fig. 13).

Recently Fernandes & Queiros (1971) also counted $2n = 40$ chromosomes for *Centaurea ornata* Willd., gathered in Bragança (Portugal) on Mt San Bartolomeu. They do not give any details as to the size of the flowers: it would seem to concern the var. *macrocephala* Wk. or plants with flowers of intermediate size.

We studied meiosis in the population of the Alfacar Sierra (Mo.); the chromosomes are paired in diakinesis and in metaphase I and form 10 bivalents. However, the behaviour of the chromosomes is often irregular: secondary associations, precocious separations, lagging chromosomes and chromatid bridges are frequent. In some metaphase plates we observed quadrivalents, indicating the presence of reciprocal heterozygous translocations (Figs. 8, 9, 10). As a result of these anomalies, the pollen grains are abnormal as was the case for *C. granatensis* Boiss.

However, the fact that *C. ornata* Willd. is found in numerous Mediterranean communities can be attributed to its polymorphism, its

Table 2. *Characteristic size proportions of the ten chromosomes in Centaurea ornata Willd. var. microcephala Wk.*

Refer- ence number	Locality	Heterobrachial chromosomes					Isobrachial chromosomes				
		1	2	3	4	5	6	7	8	9	10
K.	Sierra Nevada	0.46 1.07	0.62 0.93	0.45 0.86	0.30 0.77	0.22 0.71	0.30 0.71	1.00 1.53	0.92 1.37	0.90 1.05	0.88 0.94
1289	Valdemoro	c/l T _m	0.50 1.17	0.72 1.04	0.42 0.97	0.69 0.87	0.43 0.87	0.98 1.51	0.88 1.06	0.86 0.81	0.95 0.63
1336	Despeña- perros	c/l T _m	0.50 1.00	0.68 0.86	0.66 0.74	0.95 1.50	0.91 1.19	0.88 1.10	0.93 1.03	0.95 0.80	0.77 0.81
1306	Gabaldón	c/l T _m	0.67 1.05	0.45 0.88	0.56 0.72	0.93 1.61	0.87 1.04	0.90 0.98	0.86 0.96	0.86 0.92	0.82 0.73

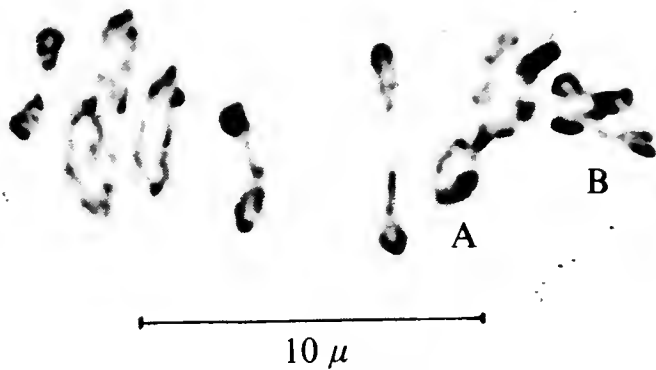
T_m, proportion of the total length of each chromosome to the mean length of the whole metaphase plate chromosome.

c/l, proportion for each chromosome of short to long arms. When c/l is lower than 0.75 there is a heterobrachial chromosome, and when c/l is equal to or greater than 0.75 there is an isobrachial chromosome.

These proportions represent the mean of thirty metaphase plate measurements.

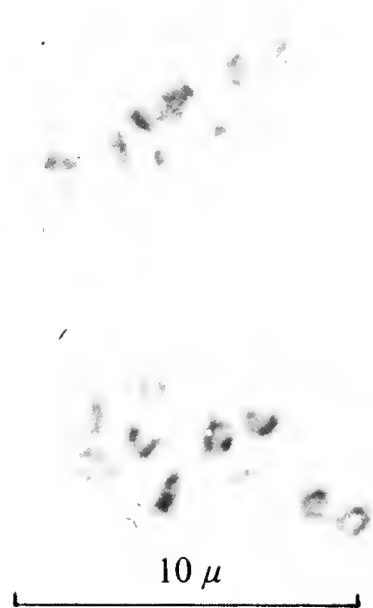
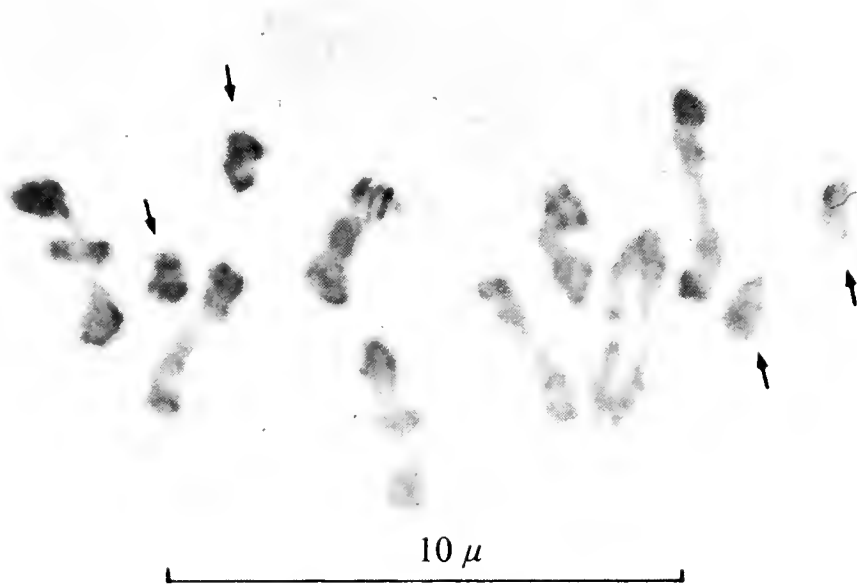
Chromosomes with satellites are enclosed in a box.

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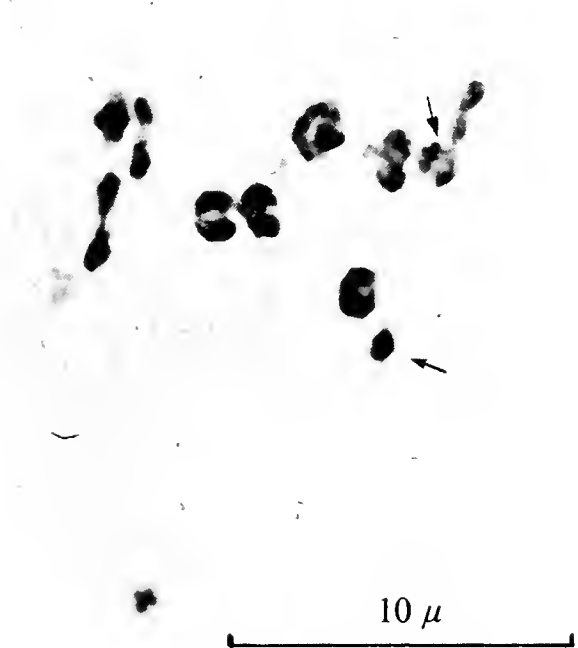
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Figs. 6 and 7. Irregular meiosis in *C. granatensis* Boiss., population Gr., $2n = 20$. In Fig. 6 the 20 chromosomes form 6 bivalents and 2 quadrivalents, one of them indicating the beginning of the formation of a ring of four chromosomes (A), the other one a zigzag chain of four other chromosomes, signs of translocation heterozygote (B). In Fig. 7 the 20 chromosomes form 8 bivalents and 4 univalents (indicated with an arrow).

Figs. 8, 9 and 10. Irregular meiosis in *C. ornata* Willd. var. *microcephala* Wk., population Mo, $2n = 20$. Fig. 8, anaphase I with chromatid bridges; Fig. 9, metaphase I with a cross-shaped quadrivalent, sign of a translocation heterozygote (indicated by an arrow); Fig. 10, metaphase I, the 20 chromosomes form 9 bivalents and 2 univalents (indicated by an arrow).

12



13



14

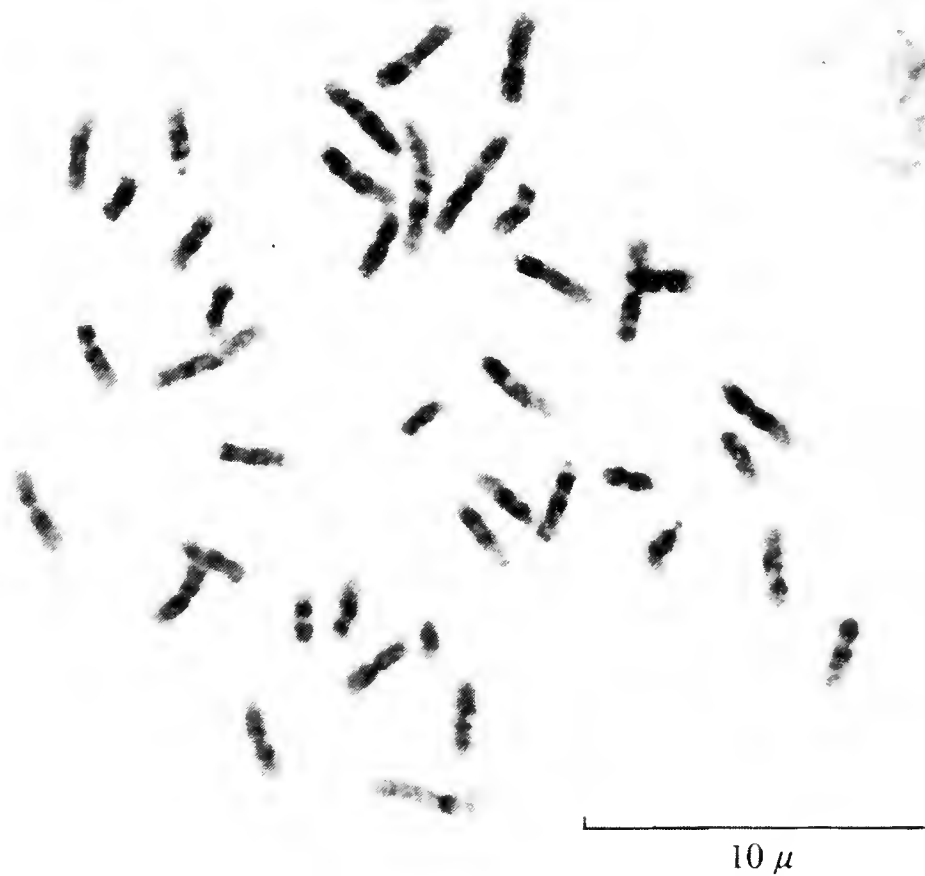


Fig. 12. Somatic chromosomes of *C. ornata* Willd. var. *microcephala* Wk., population K., $2n = 20$.

Fig. 13. Somatic chromosomes of *C. ornata* Willd. var. *macrocephala* Wk., population 1337, $2n = 40+5B$ (the supernumerary chromosomes indicated by an arrow).

Fig. 14. Somatic chromosomes of *C. ornata* Willd., morphological intermediate form, population 1295, $2n = 40$.

variable karyotype and its occasionally irregular meiosis. It is probably a taxon undergoing transformation. A more extensive study of a large number of populations in the whole Iberian peninsula would cast light on the genetic problems revealed by the karyological study.

(3) *Centaurea saxicola* Lag.

This taxon is only found in the south-east of Spain: it is, as its name indicates, a saxicolous species. Rivas-Goday (1962) considers that it is a characteristic species of the *Asplenietea rupestris* in the sierras of Callosa, Segura, Orihuela, Crevillente, Carthagená and Carrascoe. We have gathered these plants in the following place:

1326-7: Callosa de Segura, province of Alicante, calcareous rocky walls above St Roch Church, about 100 m altitude.

In this population there were two kinds of plants:

(a) Some of them were prostrate with short stems (1326), agreeing with the type *Centaurea saxicola* Lag. var. *saxicola*. We counted on them $2n = 60+2-4 B$ (Fig. 15), Gardou (1972).

(b) The other ones (1327) were tallest with longer stems, according to the diagnosis of Esteve-Chueca (1965) *Centaurea saxicola* Lag. var. *littorale* Est.-Chu. On these plants we observed $2n = 60$ chromosomes without supernumerary chromosomes (Fig. 16), Gardou (1972).

We consider that *C. saxicola* Lag. is a hexaploid and that the supernumerary chromosomes represent the only size difference between the two kinds of plants forming the two varieties. In this way it is not right to speak about two varieties in *C. saxicola* Lag., we only have two forms of the same species.

Morphologically these taxa are very close to *Centaurea ornata* Willd. and both species present supernumerary chromosomes. It is difficult to compare idiograms of both species because we have seen that there were variable karyotypes in *C. ornata* Willd. But we think that *C. saxicola* Lag. could have originated from hybridizations between diploid and tetraploid *C. ornata* Willd.

SECTION *Cyanus* CASS.

We studied 6 populations belonging to this section in the following localities:

1236: Mont Lachens (France), Var, south slope near the top about 1700 m altitude; $2n = 40$ (Fig. 3).

1293: Sierra de Guadarrama (Spain), province of Madrid, between Navacerrada and Cercedilla, about 1200 m altitude; $2n = 20$ (Fig. 4).

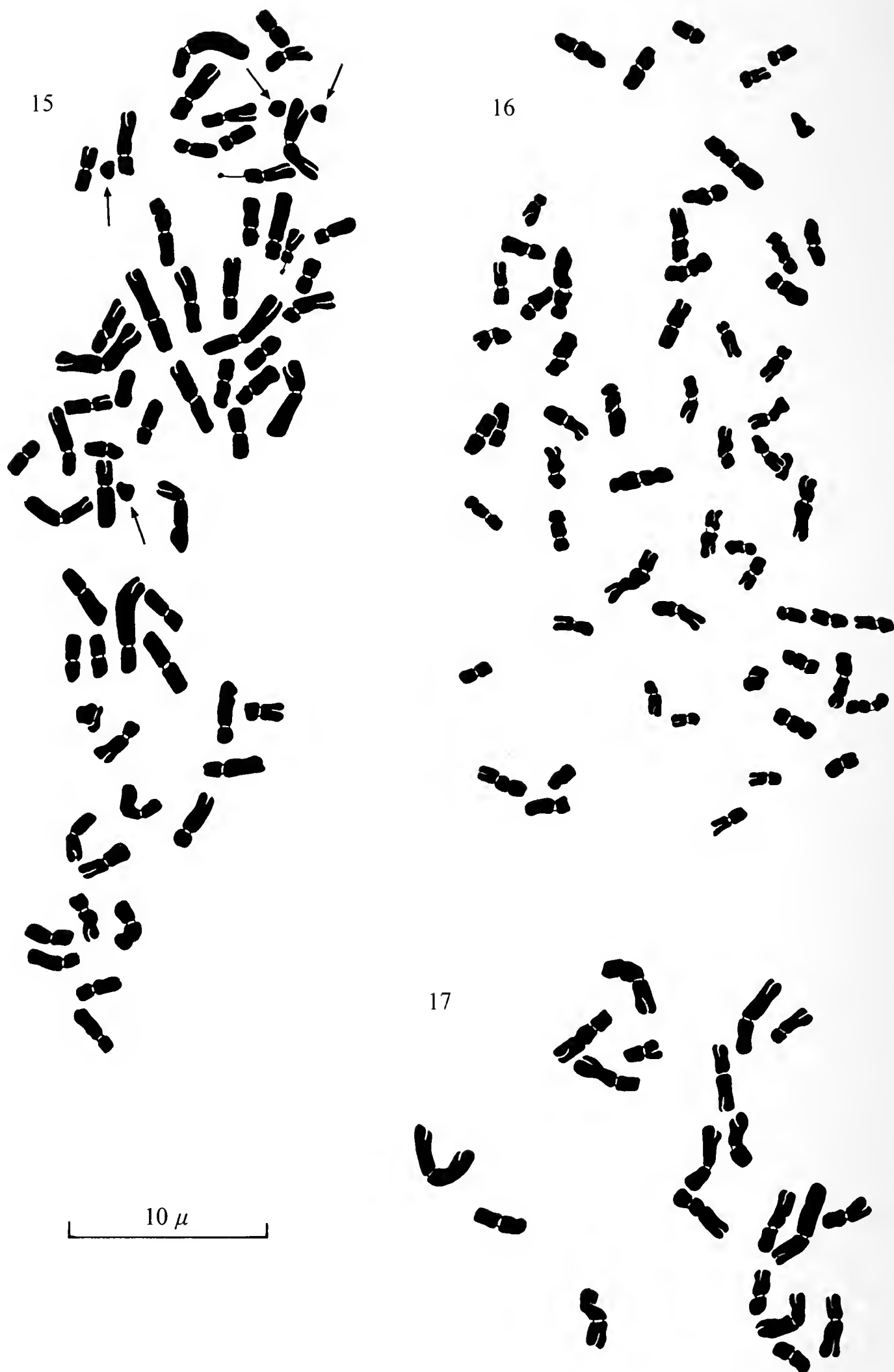


Fig. 15. Somatic chromosomes of *C. saxicola* Lag. var. *saxicola*, population 1326, $2n = 60+4B$ (supernumerary chromosomes indicated by an arrow).

Fig. 16. Somatic chromosomes of *C. saxicola* Lag. var. *littorale* Est.-Chu., population 1327, $2n = 60$.

Fig. 17. Somatic chromosomes of *C. granatensis* Boiss., population 1456, $2n = 20$.

C. 7: Sierra Nevada (Spain), province of Granada, Dehesa de Dilar, near the river Dilar in the side of the path, about 1800 m altitude; $n = 10$ (Fig. 22).

C. 91: Sierra de Tejeda (Spain), province of Granada, on the nearest mountain in the side of the farms of the Hoyos gardens, about 1700 m altitude, calcareous soil; $2n = 20$.

1376: Djebel Azrou Akchar (Morocco), eastern part of the Rif, calcareous rocks near the top, about 2020 m altitude; $2n = 20$.

1437: Djebel Ayachi (Morocco), eastern part of the Haut Atlas, Imi-n-Thand valley, calcareous crumbled-down stones, under the cedar woods, about 2500 m altitude; $2n = 20$.

All these populations can be classified in the polymorphous taxon *Centaurea variegata* Lmk. (Lamarck, *Encycl. méth.* 1: 668 (1784)) = *C. lingulata* Lag. (Lagasca, *Gen. et spec. pl. nov.* p. 32; 1816) = *C. triumfetti* All. var. *seuseana* Gugler (Gugler in Schinz & Keller, *Fl. Schw.* ed. 3, 2: 353 (1914)).

This perimediterranean calcicolous taxon possesses a very wide geographical area of distribution. In the western Mediterranean basin it occurs frequently in the south of France (Provence Alps), Spain, Italy, Greece and Morocco. In the eastern Mediterranean basin the total distribution is larger, including Turkey, Syria, Lebanon and eastwards to Armenia and Iran. Within the whole area this taxon occurs on calcareous rocky steppes except for the Guadarrama population (1293) in Spain which is in a siliceous forest community.

Five of the six populations are diploid: they are gathered from Morocco and Spain. We observed mitosis in populations 1293, 1376, 1437 and C. 91 with $2n = 20$ chromosomes and meiosis with $n = 10$ chromosomes in the C. 7 population.

In the metaphase plate mitosis, 6 pairs of chromosomes are heterobrachial, 2 of which are satellite-bearing, and 4 pairs are isobrachial. In the meiosis the chromosomes are paired in diakinesis and in metaphase I forming 10 bivalents normally (Fig. 22). But they sometimes form secondary associations and show chromatid bridges in the first anaphase. We think that it is a stable diploid. It seems that secondary associations are the trace of an aneuploid origin.

The sixth population we studied was tetraploid with $2n = 40$ chromosomes amongst which there were four satellite chromosomes: it was the French population of Mont Lachens (1236).

From this study we can deduce that the basic chromosome number of these plants is $x = 10$. In Spain and in Morocco the plant populations are diploid: in these countries different authors named them *C. variegata* Lmk. or *C. lingulata* Lag. On the other hand the south of France population is a tetraploid one and Briquet (1931) named it *C. triumfetti* All. var. *seuseana* Gugler. But all these six populations are morphologically identical and we can group them under the same name

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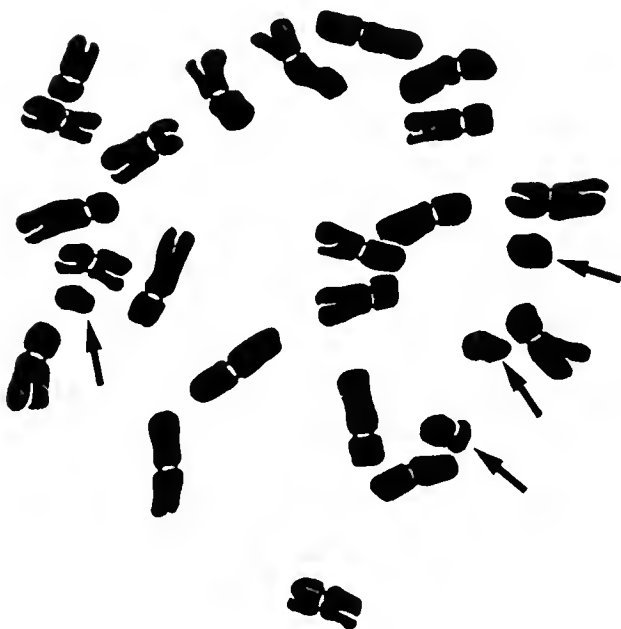
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21



20

10 μ

22



Fig. 18. Somatic chromosomes of *C. aspera* L. ssp. *stenophylla* Wk., population 1309, $2n = 22$.

Fig. 19. Somatic chromosomes of *C. aspera* L. ssp. *subinermis* DC., population 1297 b, $2n = 22$.

Fig. 20. Somatic chromosomes of *C. aspera* L. ssp. *subinermis* DC., population 1452, $2n = 22 + 4B$ (supernumerary chromosomes indicated by an arrow).

Fig. 21. Chromosome pairing at first metaphase of meiosis, 11 bivalents, in *C. aspera* L. ssp. *subinermis* DC., population Ca., $n = 11$.

Fig. 22. Chromosome pairing at first metaphase of meiosis, 10 bivalents, in *C. variegata* Lmk., population C. 7, $n = 10$.

of *Centaurea variegata* Lmk., the oldest one. This taxon is represented by diploid and tetraploid populations all along its geographical area.

Thus, in the section *Cyanus* Cass., there are three basic chromosome numbers $x = 10$, $x = 11$ and $x = 12$.

(1) The first one with $x = 10$ is represented by diploid and tetraploid taxa as we have seen before. It is *C. variegata* Lmk. that we can connect with the oriental species of this group *C. fischeri* Willd. var. *ochroleuca* (Willd.) Grossh. with $2n = 40$ according to Podubnaja-Arnoldi (1931) and Tonian (1968) and *C. huetii* Boiss. with $2n = 40+2$ B according to Tonian (1968).

(2) The second one, with $x = 11$, is also represented by diploid and tetraploid taxa. They can be connected with *C. triumphetti* All. and *C. montana* L. according to the results of Guinochet (1957) and Baksay (1957).

(3) The third one known, with $x = 12$, is only composed of annual diploid herbs: it concerns *C. cyanus* L. s.s.

The position of the oriental species *C. depressa* Bieb. is difficult to solve in this way, because its chromosome number, $2n = 16$, (Chouk-sanova, Sveshnikova & Alexandrova, 1968 and Tonian, 1968) does not correspond to any series amongst the three previously cited.

SECTION *Seridia* JUSS.

In this section we have only studied *C. aspera* L. from Spain. Most of the plants of this species are remarkably variable herbs. In this way Willkomm (1870) mentioned four subspecies in Spain. The first one, *C. aspera* L. ssp. *aspera*, grows widely in south-west Europe: it is the best known one, diploid with $2n = 22$ chromosomes according to the results of Maude (1939), Fahmy (1951), Guinochet (1957), Fernandes & Queiros (1971), van Loon (1971) and Gardou (1972).

We studied the karyology of five populations belonging to two subspecies in the east and south-east of Spain as follows:

(1) *C. aspera* L. ssp. *stenophylla* Wk.

1309: El Palmar, province of Valencia, grassland between La Albufera and El Palmar; $2n = 22$ (Fig. 18).

1311: La Albufera, province of Valencia, nearer the ranch of El Saler; $2n = 22$.

(2) *C. aspera* L. ssp. *subinermis* DC.

1297 b: Arganda, province of Madrid, along the road; $2n = 22$ (Fig. 19).

1452: Venta de las Angustias, province of Granada, 37 km south of Granada, between Beznar and Tablate; $2n = 22+0-4$ B (Fig. 20).

Ca.: Lecrin valley, province of Granada, south-west of Sierra Nevada; $2n = 22$, $n = 11$ (Fig. 21).

The two subspecies studied are diploid as was the case for *C. aspera* L. ssp. *aspera*. Only the population 1452 presents 0–4 supernumerary chromosomes.

In meiosis, for example in the Ca. population, the chromosomes are regularly associated showing 11 bivalents (Fig. 21). It seems to be a stable diploid. Consequently the endemism and the polymorphism of these Spanish subspecies only occur at the diploid level.

Thus, in these taxa, we cannot find a parallelism between the morphological polymorphism and the karyological regularity except for the population showing supernumerary chromosomes.

CONCLUSION

Some taxa belonging to three sections of the genus *Centaurea* L. were studied in this report. We found that the relationship between chromosomal problems and endemism is different from one taxon to another.

We also think that the origin of the great number of endemic *Centaurea* L. species of these sections in south-east Spain can perhaps be found in the reciprocal translocation mechanism.

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STUDIES IN THE GENUS *CROCUS*

B. Mathew and C. A. Brighton

ABSTRACT

A unique collection of about 90 species of *Crocus*, mostly of known wild origin, has been assembled at Kew and is being used as the basis for a revision of the genus. The cytology of nearly all the species is being studied comprehensively for the first time using natural source material, and it is hoped that this, together with a critical examination of the morphological details, will assist in a more satisfactory classification than is at present available.

Dr E. F. Warburg in 1957 terminated a paper on *Crocus* species with the statement 'It seems impossible with the present information to get any picture of the probable evolution within the group or to devise a really satisfactory classification.' Unfortunately there has never been a really thorough review of the genus, including disciplines such as morphology and cytology, and although a beautiful monograph by Maw (1886) exists, many new species have been described since then and the genus is in need of careful revision. The first real attempt to study the genus as a whole in recent times was by Mather and Collins at the John Innes Institute in the 1930s. Mather (1932) did publish much cytological data; unfortunately, in many cases it was based on plants of unknown wild origin, and probably no voucher specimens exist, making it impossible to check back on their material. Sadly, Collins died before any of his taxonomic work was published.

At Kew we have in cultivation about 900 collections of *Crocus*, representing 90 of the 100 known species. Many of these have been studied and collected in their wild habitats by us. Originally it was intended to revise the genus on a geographical basis for each of the Floras currently in preparation (i.e. Flora Europaea, Flora of Turkey, Flora Iranica, Flora of Iraq) but it was obvious that such a valuable living collection had a much greater potential for a complete cytotaxonomic study, and a revision of the whole genus is now envisaged.

Crocus is an Old World genus, distributed from Portugal in the west to Russian Tadzhikistan and Afghanistan in the east, and from Poland in the north as far south as North Africa and Israel. In Europe it is a

genus mainly of the mountain areas, although in terms of altitude the species on the whole do not reach the alpine zones, preferring the rocky, drier foothills. There are a large number of species in the Balkan region, for example, along the Adriatic coastal mountains of Yugoslavia, the northern Aegean and especially in the Peloponnese and the Greek islands. Also the Mediterranean climate areas of western and southern Turkey contain a large number of species. This great concentration of species in the Balkans has led to the speculation that the origins of the genus lie within this area (e.g. Maw, Feinbrun, Bate-Smith, 1968, 1969). Others (e.g. Bowles, 1924, Greuter, 1968) favour the theory that the origins lie in Africa, since the characters of *Crocus*, in particular the cormous state and the subterranean ovary, are almost certainly an adaptation to dry arid conditions. The little-known *C. boulosii* Greuter from Cyrenaica adds weight to this theory, since Greuter considers it to be a primitive species. It seems probable that the origins of *Crocus* lie in a *Romulea*-like plant. *Romulea* is a related genus, the northern hemisphere species of which, unlike *Crocus*, have an aerial, not subterranean, ovary. Goldblatt (1971) considers that if the origins of *Crocus* are in a *Romulea*-type plant, the species with a high number of small chromosomes are the most primitive. *C. carpetanus* from Spain has a count of $2n = 64$ and has a leaf quite unlike the rest of the *Crocus* species, being semi-terete and more like some *Romulea* species. It is possible, therefore, that *Crocus* originated in Africa and migrated to Europe via the Iberian peninsula, *C. boulosii* and *C. carpetanus* from Libya and Spain respectively representing the most primitive species now in existence.

From the point of view of a practical system of classification for Flora purposes and field identification, *Crocus* species exhibit a remarkable range of characters. The corm tunics are extremely important and the gross morphological features of these represent some of the major dividing lines between the groups of species. Unfortunately with the corm tunic, as with virtually all other known characters in the genus, no hard and fast dividing lines can be made between the groups of species, and there always remain a few species which do not really fit into any group or section. The tunic may consist of a mass of fine or coarse fibres, these either netted (Reticulati section of Maw), interwoven (Intertexti) or parallel (Fibromembranacei). It may be membranous or coriaceous without obvious fibres, sometimes the base splitting off as horizontal rings (Annulati), or splitting vertically into strips of tissue. Although such major differences would appear to give an excellent basis for subdividing the genus, it is a very artificial system, for the differences between the tunics of species within, for example, the reticulate group are as striking as those between some of the groups

themselves. Perhaps even more fundamental is the absence or presence of a basal spathe subtending the flower. Herbert (1847) used this character to form his divisions *Nudiflori* and *Involucrati*. Here again, however, this has been shown to be not entirely reliable, and in populations of some species it would appear that plants with and without this spathe occur. Herbert had trouble with this character for he had a third division, *Subnudi*, into which he placed the species with an imperfectly formed spathe, regarding these as the transition point between the two divisions. The bract and bracteole which arise at the base of the ovary (the 'proper spathe' of many authors) also provide a useful method of distinguishing the species. The bracteole can be equal to the bract, much reduced or absent altogether. Although very useful at specific level there is probably no greater significance in this and the absence or presence does not represent any fundamental division within the genus. The degree of division of the style into distinct arms varies from trilobed in its simplest form to much-dissected, and here again this provides good distinguishing features at specific level. Baker (1873) used this to form his subgroups *Holostigma*, *Odontostigma* and *Schizostigma*, but there are so many in-between stages of division that it is considered impossible to use this at a higher rank than that of species.

These comments apply to almost any character or group of characters which has so far been chosen, and although some sizeable units made up of closely related taxa exist within the genus, there are always several species which do not readily fit into the groups.

The studies at Kew include a comprehensive survey of *Crocus* seed characters using the scanning electron microscope, and at the present stage the results are promising, for the surface architecture varies enormously throughout the genus. Pollen studies show that the external morphology is not critical from a taxonomic point of view, although Schulze (1970) found that the pollen could be spiraperturate or non-aperturate. A full study of all the species is necessary before it becomes clear if this coincides with any other character. Certainly, of those ten species studied by Schulze (1970), the five with spiraperturate pollen were in section *Nudiflori* and the five with non-aperturate pollen belonged to section *Involucrati*.

The leaf characters have been studied recently by Culling (1972), and as a result of this comprehensive survey it was suggested that there might be as many as ten groups of related species within the genus. However, the same problem occurs with leaf features as was mentioned above with other characters, that some species do not readily fit into any grouping.

It is obviously essential that as much data as possible about all the

species are acquired before any attempt can be made to make accurate suggestions regarding evolutionary trends, or to construct a fundamental classification. At specific level, however, for the practical purposes of Flora accounts the morphological study at Kew is well advanced.

CYTOLOGY

A large number of chromosome counts have already been published for the genus *Crocus*. Mather (1932), Pathak (1940) and Karasawa (1932–56) have contributed the main part of this work, but their material was of unspecified origin and we do not have herbarium material at our disposal. In order to study natural evolution one must look at plants in their natural state, and a knowledge of localities will also make it possible to determine distributions of basic numbers, chromosome races and possible lines of evolutionary development.

The earlier workers showed that *Crocus* is an extremely variable genus, both in chromosome numbers and karyotype morphology. Until recently it was not known whether this reflected the state of the genus in the wild. Feinbrun (1957, 1958) and Sopova (1972) made the first chromosome counts from material from known wild sources and showed that the genus is indeed a very variable one.

At Kew we have approximately 900 collections of some 90 species, all from known wild origins extending over the entire range of distribution, and this has enabled us to obtain a much more comprehensive picture of *Crocus* as it occurs in the wild. The initial list of chromosome counts for 88 species has been published (Brighton, Mathew & Marchant, 1973), and shows a great range of chromosome numbers including some intraspecific variation. Our results both confirm and extend those of earlier workers.

Our investigation has shown that *Crocus* has chromosome numbers of $2n = 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 34, 44, 48$ and 64 . We also found that B-chromosomes occurred in some species, the highest number recorded being 11. This wide range of numbers is unusual, though not unique in the monocotyledons. In the Iridaceae, for example, *Iris* also has a range of numbers from $2n = 16$ to $2n = 84$; while in the Liliaceae the chromosome numbers of *Ornithogalum* range from $2n = 6$ to $2n = 58$, and those of *Scilla* from $2n = 10$ to $2n = 54$.

As well as the numerical variation we also observed substantial interspecific differences in chromosome morphology. Karyotypes are being prepared and will be published in due course.

Some species show a marked stability in their karyotype characteris-

tics. For example, *C. flavus* ($2n = 8$) has four pairs of large submedian chromosomes and a distinctive secondary constriction in the shorter arms of one pair which makes the karyotype easily recognizable. *C. olivieri* ($2n = 6$) has three pairs of large subterminal chromosomes with a small secondary constriction next to the centromere of one pair of chromosomes. Again it is an immediately recognizable karyotype, completely different from *C. flavus*, which can provide the taxonomist with important information when classifying his specimens.

In addition to interspecific variation we have also found intraspecific differences in some species. In *C. cancellatus*, for example, we have plants with $2n = 8, 10, 12$ and 16 chromosomes. B-chromosomes also occur in this group. Further variation was found in the karyotype morphology of the plants with $2n = 8$ and 10 . In both there were two distinct karyotypes. Those of the $2n = 12$ and $2n = 16$ plants were all constant. It is hoped that with the *C. cancellatus* agg. we will be able to correlate the cytological differences with those of phenotype and geographical distribution which may resolve the group into several taxa.

C. heuffelianus presents us with a greater problem, as there are no obvious characters which can be correlated with the differences in chromosome number. In this species somatic numbers of $2n = 8, 10, 12, 18, 20, 22$ and 23 have been found, and mixed populations are known to occur. Population samples have been taken and a more comprehensive study is in progress.

Intraspecific variation of this kind was also found in *Ornithogalum* by Cullen & Ratter (1967).

In a variable genus like *Crocus* one must consider the possible existence of polyploidy, especially in the higher numbers. From studies of the karyotypes it has been impossible to determine a polyploid series or polyploid relationships within groups, but it is hoped that meiotic studies will throw more light on this problem.

A study of this kind illustrates that in looking at material from natural populations one can obtain a more realistic picture of the genus, and that close co-operation between cytological and taxonomic disciplines can be very profitable. We hope that continued studies along these lines will enable us to classify *Crocus* adequately and provide useful evidence on lines of evolution.

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STUDIES IN THE GENUS *MYOSOTIS*

J. Grau

ABSTRACT

The paper considers the value of cytological studies in elucidating taxonomic and evolutionary relationships in the genus *Myosotis* in Europe. Information is given on *M. decumbens* and its distinction from *M. sylvatica*; the former has not previously been recognized as a member of the British flora, and its old herbarium records from Scotland need verification.

The genus *Myosotis* – the forget-me-nots – is so well known that it might be unnecessary to explain what a *Myosotis* looks like. There is a great resemblance in at least most of the European species, and this causes some problems in determining some of the species.

Though the genus also has a considerable part of its area in the southern hemisphere, especially in Australia and New Zealand, I want to restrict my lecture to the European species. To clear up the connections and to give some hints for a better circumscription of the species, cytology was of great help. I want to explain in the two parts of my talk what seems to be behind this great similarity of species. I also want to demonstrate that the Mediterranean area is of great use in solving Central European systematic problems.

The genus *Myosotis* is represented in Europe by three ecological groups. The first of these groups consists of perennial species which grow in woody or alpine areas. A second group prefers very humid areas; these are the marsh forget-me-nots such as *Myosotis scorpioides* and *M. caespitosa*. The only thing I want to say about this group here is that it forms a polyploid series ending with octoploid species. The third group consists of annual herbs which have their centre of distribution certainly in the Mediterranean area but spread into Central Europe too. These species can again be subdivided into three units with clearly different centres of origin.

The first subgroup certainly originates in the Aegean area. It has only straight hairs covering the whole plant. The northernmost place where it can be found is southern France. All five species of this subgroup have 24 chromosomes. (I have to digress here to say a few words

concerning the chromosome numbers of *Myosotis*. In the *Boraginaceae* the basic number $x = 12$ is very frequent. It is also to be found in many of the species of *Myosotis* and this number must be without any doubt the primary basic number of this genus. In many cases it is possible to show how from this secondary basic numbers can rise. One example of this I want to show later on. Going back to our first subgroup we can say now that all its species are diploid.)

In the second subgroup, the centre of which is a little further to the east and which is distributed more widely, all parts of the plant have hooked hairs. Now this group has a very strange type of distribution. It is to be found in spots and very limited areas towards the west up to the Sierra Nevada in southern Spain. Strangely enough the two most important species of this group have been described from these most remote places of growth. Cytologically this group is more variable, that is to say we can find diploids and polyploids, euploids and aneuploids.

A third subgroup has its centre on the Iberian peninsula. This group is distinguished by its yellow flowers and very large pollen grains. It consists of a polyploid series up to hexaploid species with 72 chromosomes. This hexaploid species is the only one in Central Europe and is of rare occurrence in northern and eastern Europe.

After this subdivision only a few annual taxa are left which do not fit into this system. *M. ramosissima* is one of these species. It shows a little focus in western Europe, and one of its subspecies reaches in a typical Atlantic distribution from Portugal via France to southern England. This is the subspecies *globularioides* with different calyces and nutlets. In *M. ramosissima* s.l. only polyploids exist. Perhaps they are allopolyploids connecting the groups mentioned above.

The second species which belongs to the annuals and also does not fit into the three subgroups is *M. arvensis*. But it seems that this species is, unlike the above-mentioned species, a secondary annual and derives from perennials as we shall see later on.

A diagram (Fig. 1) gives a summary of the groups mentioned. On the left the euploids – on the right the few aneuploids, at the bottom the diploid Mediterranean species, at the top the mainly northern polyploids. These show moreover a widespread distribution while the Mediterranean diploids are found to be more or less local without a coherent area. *M. arvensis* does not really belong to the annuals, as I said before, and therefore it leads to the second part of my talk.

This part concerns the perennials of alpine or woody habitats. In contrast to the annuals, which are quite satisfactorily distinguished and classified, in these species the poverty of characters is so great that at

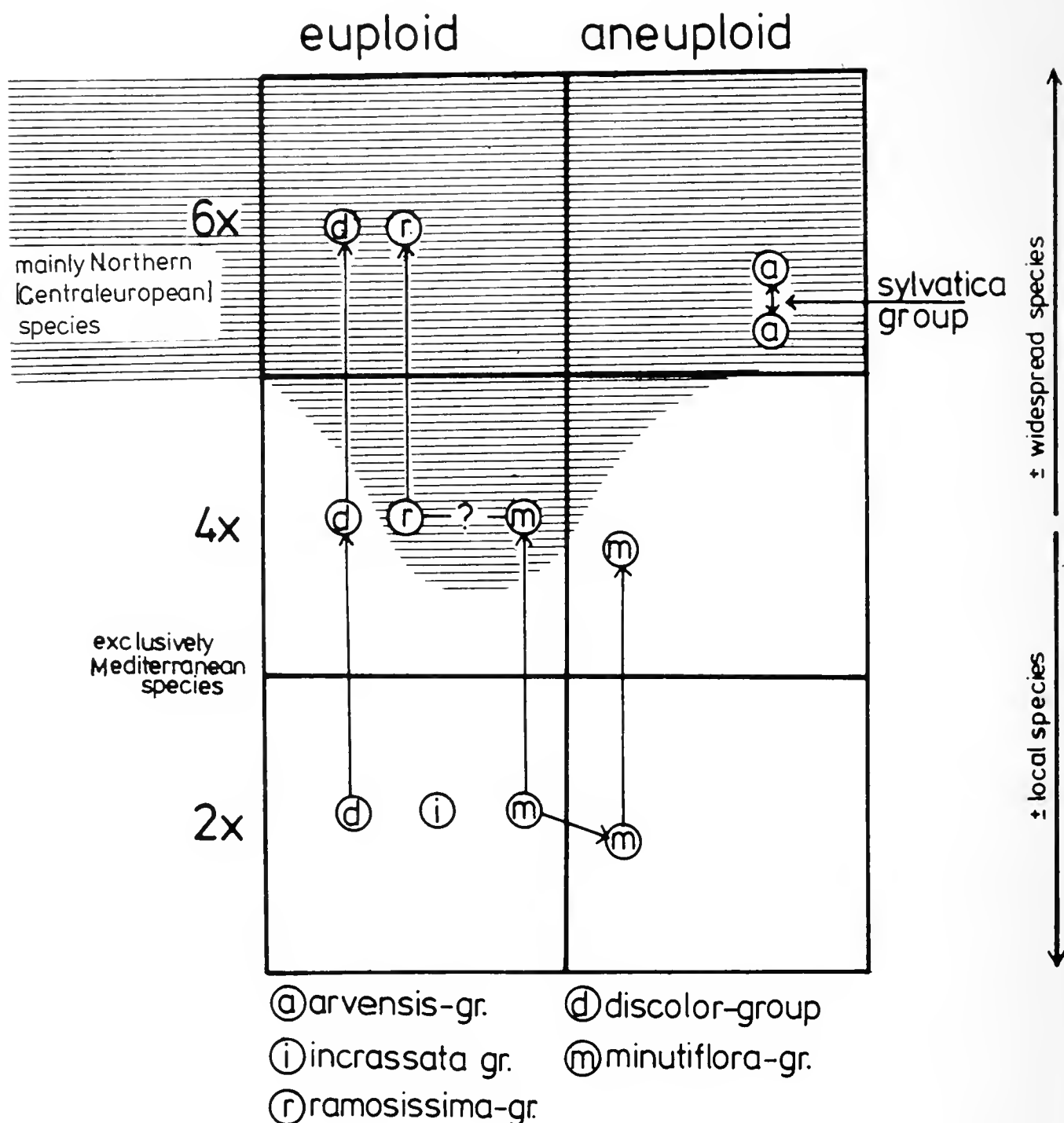


Fig. 1. Diagram showing cytological relationships and geographical distribution of annual species of *Myosotis*.

least sometimes there has been the tendency to treat them as only one aggregate. Only a cytological investigation, which showed very many different chromosome numbers, brought the possibility of a clear separation of species in quite a number of cases.

To explain this I have to detail a little the morphology of chromosomes in *Myosotis*. We can distinguish two chromosome types within the European species: metacentric ones with more or less equivalent arms, and acrocentric ones with a very reduced second arm. This second type especially is very remarkable and can be used to characterize the chromosome sets. The perennial species I talk about can roughly be divided into two groups. Within the alpestris group there

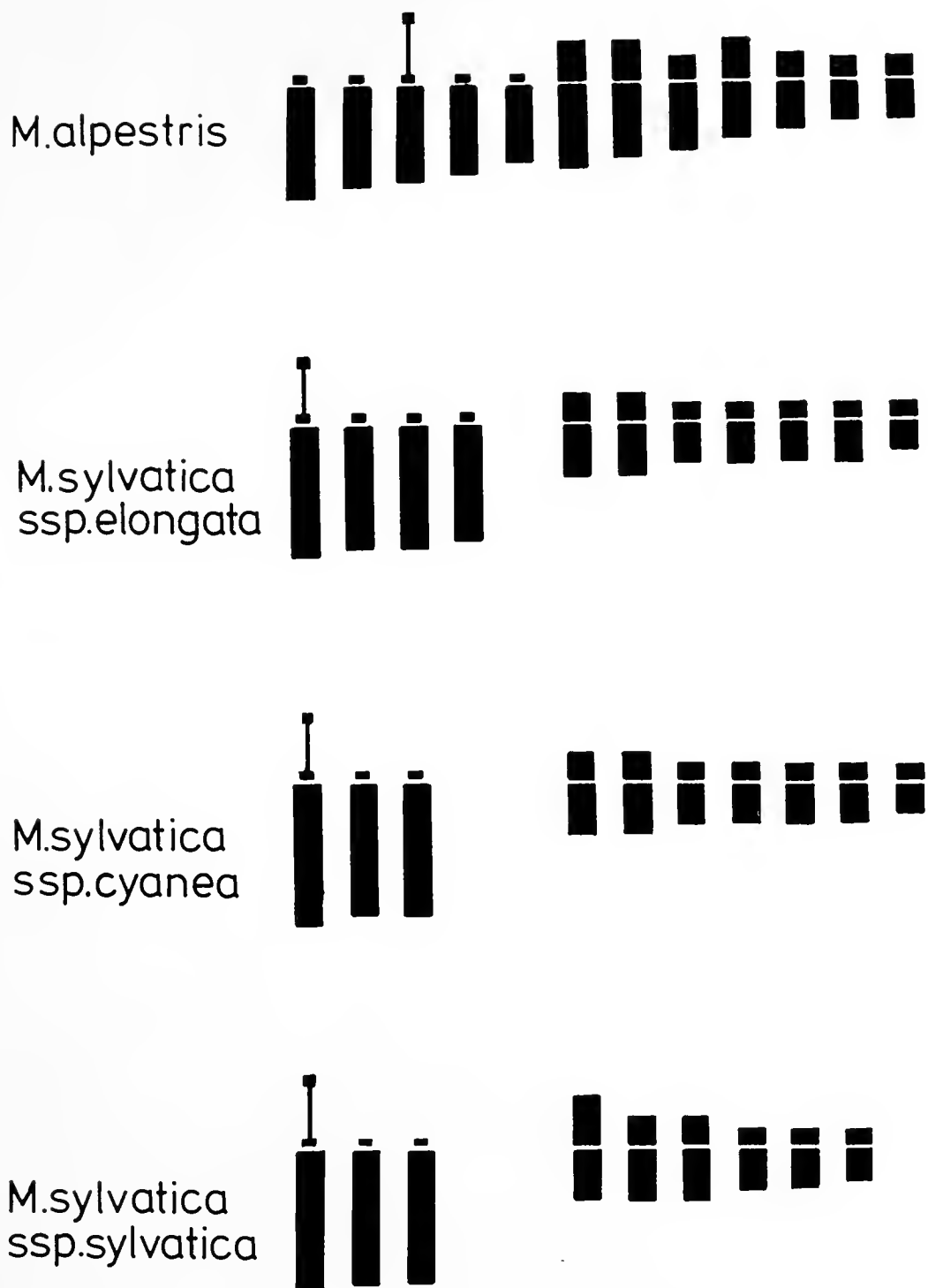


Fig. 2. The karyotypes of different perennial species of *Myosotis*. On the left the acrocentric chromosomes, on the right the metacentric chromosomes.

exist diploids, tetraploids and hexaploids, which means that we have a regular polyploid series. This series is founded on the basic number $x = 12$.

The *sylvatica* group, however, shows the numbers $n = 9, 10, 11, 14, 16$ and 17 without any representative of the basis $n = 12$. This seems to be an aneuploid series with some gaps. A detailed investigation, however, showed that this series is not directly connected. The taxa with $n = 11, 10$ and 9 above all form a separate descending aneuploid series starting with an unknown ancestor with the chromosome number $n = 12$. This can very easily be explained considering the two chromosome types. We can see this in Fig. 2. I assume that we can start with

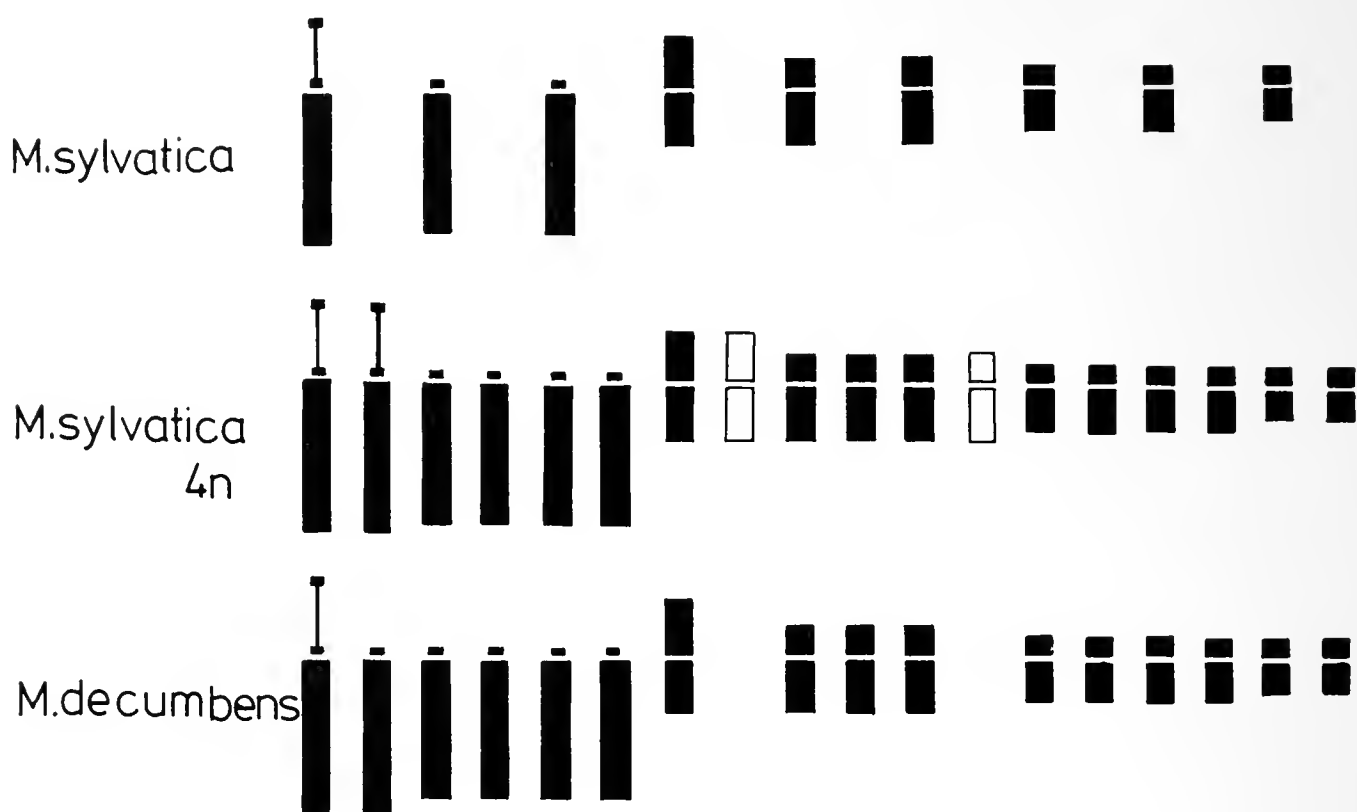


Fig. 3. The karyotype of *M. sylvatica*, of its hypothetical tetraploid form, and of *M. decumbens*. Lost chromosomes open.

a karyotype similar to that of *M. alpestris*, which has 7 metacentric and 5 acrocentric chromosomes in the haploid set. Twice in the course of the development the number of acrocentric chromosomes was reduced by one chromosome. The results of the process are the numbers of $n = 11$ and $n = 10$. In the last step finally two metacentric chromosomes fused and formed a new one with equal arms. This is the case in the type subspecies *M. sylvatica*. All taxa with these three derived numbers are very closely related and form the four subspecies of *M. sylvatica* in Europe.

But how could the chromosome number higher than the original basis 12 in the *sylvatica* group evolve? Even in this case the chromosome types are very helpful. In Fig. 3 we see again the karyotype with $n = 9$ chromosomes, the development of which we have just seen. When we imagine this chromosome set doubled we obtain the karyotype below. In other words a simple polyploidization would have occurred. Comparing this hypothetical tetraploid set of chromosomes of *M. sylvatica* with the existing set of *M. decumbens* we can find an astonishing correspondence. Only the two white marked chromosomes are missing in the lowest row. This correspondence could in my opinion be interpreted in only one way. After the polyploidization of a *sylvatica*-like plant a continued loss of chromosomes occurred down to a north Italian subspecies of *M. decumbens* which only has 14 chromosomes left.

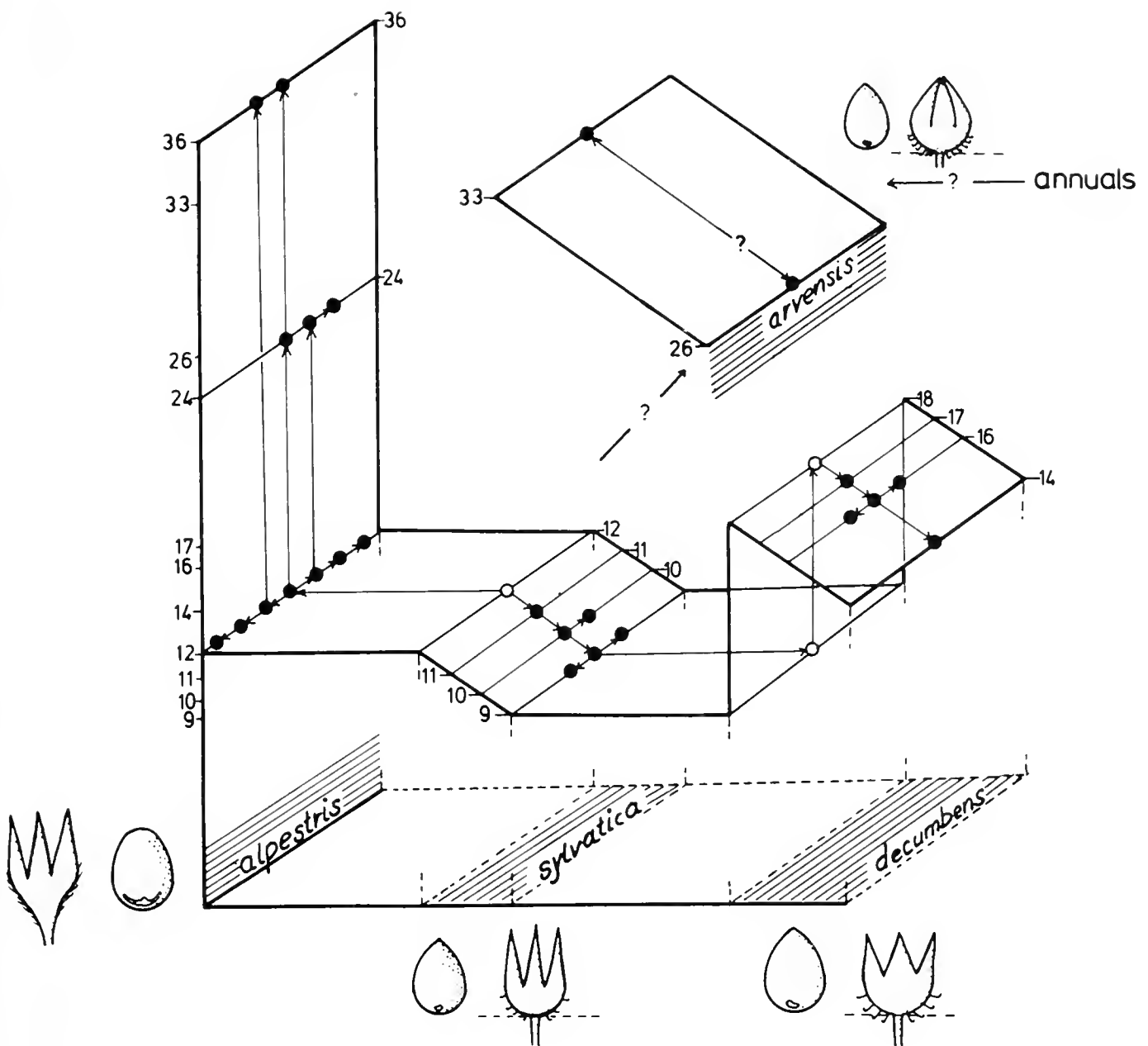


Fig. 4. Diagram showing cytological and morphological characters of the European species of the *M. sylvestica* and *M. alpestris* groups. Outline diagrams represent nutlets and fruiting calyces.

We can see the situation just described in a diagram (Fig. 4). Black dots mean existing species or subspecies, white ones hypothetical forms. On the left you will see the polyploid series of *M. alpestris* with quite a rich development of diploid species. In the middle there is the aneuploid series of *M. sylvestica*. On the right side the species and subspecies around *M. decumbens* descend down to $n = 14$. In addition I have put some of the main morphological characters on the picture. Within *M. sylvestica* and *M. decumbens* s.l. the fruiting calyces are round at the base and deciduous, with *M. alpestris* they are narrowed at the base and persistent. The nutlets of *M. alpestris* are obtuse with a large lateral folded attachment area, those of *M. sylvestica* are acute with a small attachment area. Very similar are those of *M. decumbens*. Combined with the persistence of the fruiting calyces in *M. alpestris* hooked hairs are quite rare, though always present in the two other

groups. These hairs are of different length in *M. sylvatica* and *M. decumbens*. Besides this character the calyx teeth in *M. decumbens* are broadly triangular against narrowly triangular ones in *M. sylvatica*. Also the attachment area of the nutlets in *M. decumbens* is a little larger. Also included in the diagram is the more or less ruderal, annual to biennial *M. arvensis* with its two cytologically different subspecies. This species has closed fruiting calyces which are very rich in hooked hairs, which means a better adaptation to dispersal of the fruit as a whole.

We could ask now: why is this great cytological diversity connected with such a morphological uniformity? But I think that this is not the right question to ask. Rather, we should state that it is just this uniformity which allows the cytological processes mentioned above. The first step in the development of this rather young group is a cytological change. The morphological consequences may follow later. We can see this also in the genus *Pulmonaria*, where the discrepancy of morphological and cytological behaviour is much greater.

Some further words concerning the areas of the species dealt with. *M. alpestris* is to be found, as far as Europe is concerned, in the higher mountains and sometimes uplands of continental Europe with the exception of Scandinavia. In Great Britain it exists only in Scotland and N. England. *M. sylvatica* grows in wide areas of Central Europe extending to southern Scandinavia and Great Britain. Of its cytologically more primitive subspecies the ssp. *elongata* is to be found in Sicily and southern Italy, the ssp. *cyanea* mainly in the Balkan Peninsula.

M. decumbens has a very interesting area, probably influenced by glaciation. It exists in the type subspecies in the southern half of the alpine chain, the uplands of France, the Pyrenees, northern Spain and the Sierra Nevada, and parts of Scandinavia. In Germany it grows only in the south-western part of the German Alps, the Allgäu, where we recovered it after nearly 100 years of presumed extinction. And last but not least the same situation may also exist in Great Britain. The only two records of this species originate again from Scotland, but since they also are more than a hundred years old, they need to be verified in the field. Details of the specimens are:

‘Perth, leg. Gardiner, 1846’. (M)

‘Ben Lawers, Perthshire, 18—’ (W).

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CYTOTAXONOMY OF THE GENUS *LEUCANTHEMUM* IN YUGOSLAVIA

D. Papeš

ABSTRACT

The paper reports on the cytotaxonomy of the 11 species of *Leucanthemum* occurring in Yugoslavia, and makes tentative suggestions as to their micro-evolutionary relationships.

The morphological variety and differences in chromosome number exhibited by *Leucanthemum* have attracted the interest of several cytotaxonomists during the last twenty years, yet areas remain where cytological information is lacking. This was especially true of the Yugoslav representatives, the investigations of which started only recently (Mirković, 1966, 1969; Papeš, 1971 *a*, 1971 *b*, 1972 *a*, 1972 *b*, 1972 *c* and 1973).

Leucanthemum is a highly polymorphic and widely spread genus. It grows all over Europe, North Africa and eastern Asia, and is naturalized in North America and Australia. Its polymorphic character is particularly conspicuous in Yugoslav representatives, within which we distinguished 11 species (Horvatić, 1963; Papeš, 1972 *a*), which vary also in their chromosome numbers and ploidy levels ($2x$ to $8x$) accompanied by aneuploidy and the existence of B chromosomes (Fig. 1) (Papeš, 1971 *b*, 1972 *c*).

The present paper deals with cytotaxonomy and some evolutionary aspects of possible origins and relationships of karyotypes in *Leucanthemum* species. For this purpose morphological features have been considered in conjunction with chromosome numbers, satellite form and frequency. 427 individuals belonging to 99 populations of Yugoslav *Leucanthemum* species were investigated. Cytotaxonomic methods applied here included karyological, taxonomic, morphological, ecological and phytogeographical investigations, and some study of the breeding system.

Among these 11 species from Yugoslavia only two are diploids: *L. rotundifolium* (W.K.) DC. and *L. praecox* Horvatić. *L. rotundifolium*, $2n = (2x) = 18$, is an old species, which has been completely isolated in almost all aspects from other species for a long time. It has a special morphology of leaves (Fig. 2); its locality on an old mountain –

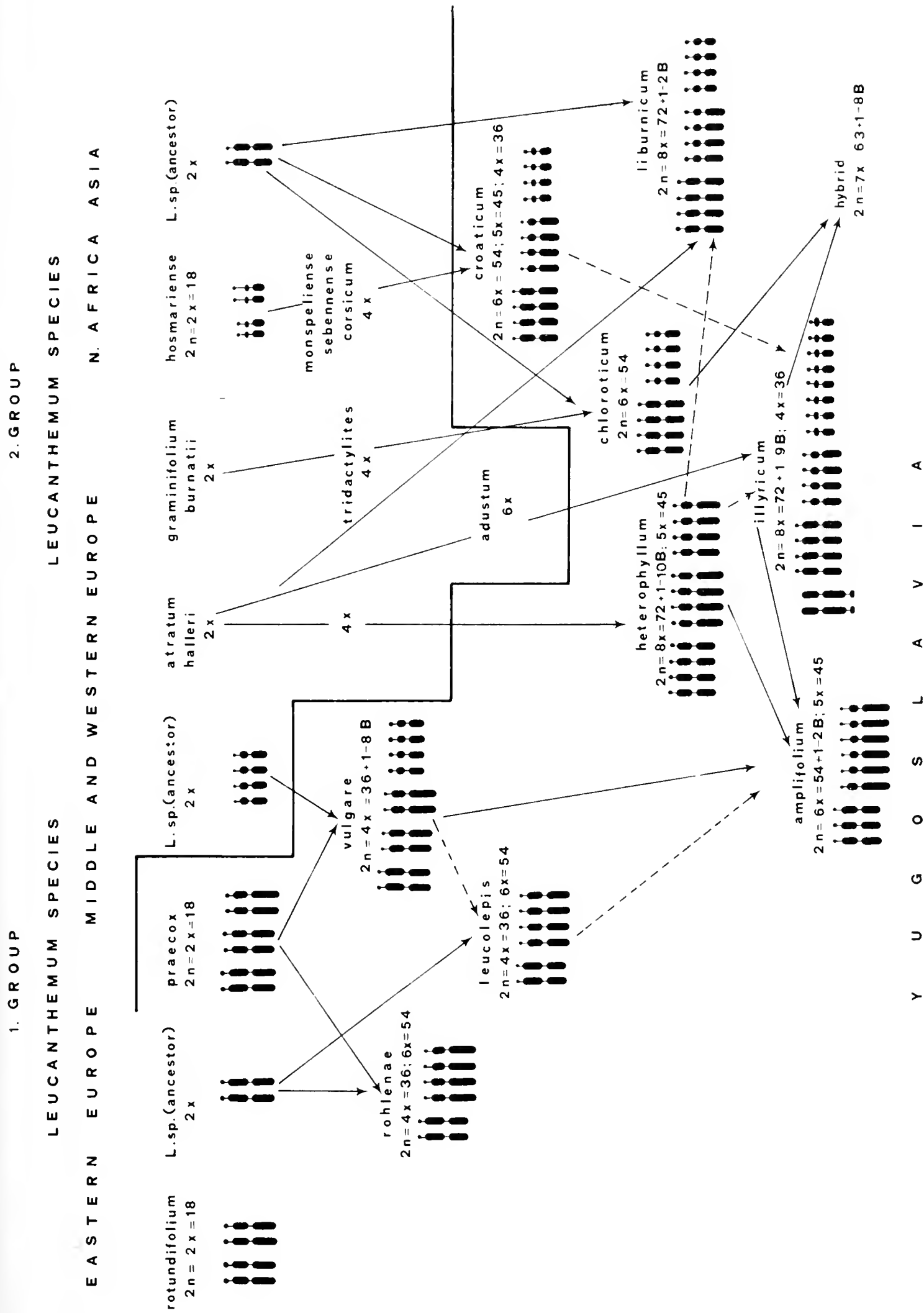


Fig. 1. Diagram of possible origins and relationships of karyotypes in *Leucanthemum* species.



Fig. 2. Leaves of stem in *Leucanthemum rotundifolium*.

Vranica in central Bosnia – is the only one in Yugoslavia. *L. rotundifolium* is the only annual, fully self-fertile species, and is therefore uniform, without any variability.

The other 10 species (Fig. 1) are mainly self-sterile, depending exclusively on outcrossing and thus capable of cross-fertilization in suitable combinations. This characteristic is responsible for the great variation of chromosome numbers among the species and even within a population of one species. In this way different levels of polyploidy arising from the basic number 9 have been found, as for instance $2x$, $4x$, $5x$, $6x$, $7x$ and $8x$, accompanied by appearance of aneuploidy and the existence of B chromosomes.

Among these 10 species only *L. praecox* Horvatić is a diploid (Fig. 3), while all other species are polyploids of hybrid origin, being either allopolyploids or autoallopolyploids. According to the results of investigations, especially the analysis of meiosis and data of the high degree of fertility, it has been stated that autopolyploids do not exist among them. In the meiosis of all polyploids, bivalents predominate over univalents and rare multivalents (which have no more than 6 chromosomes in associations).

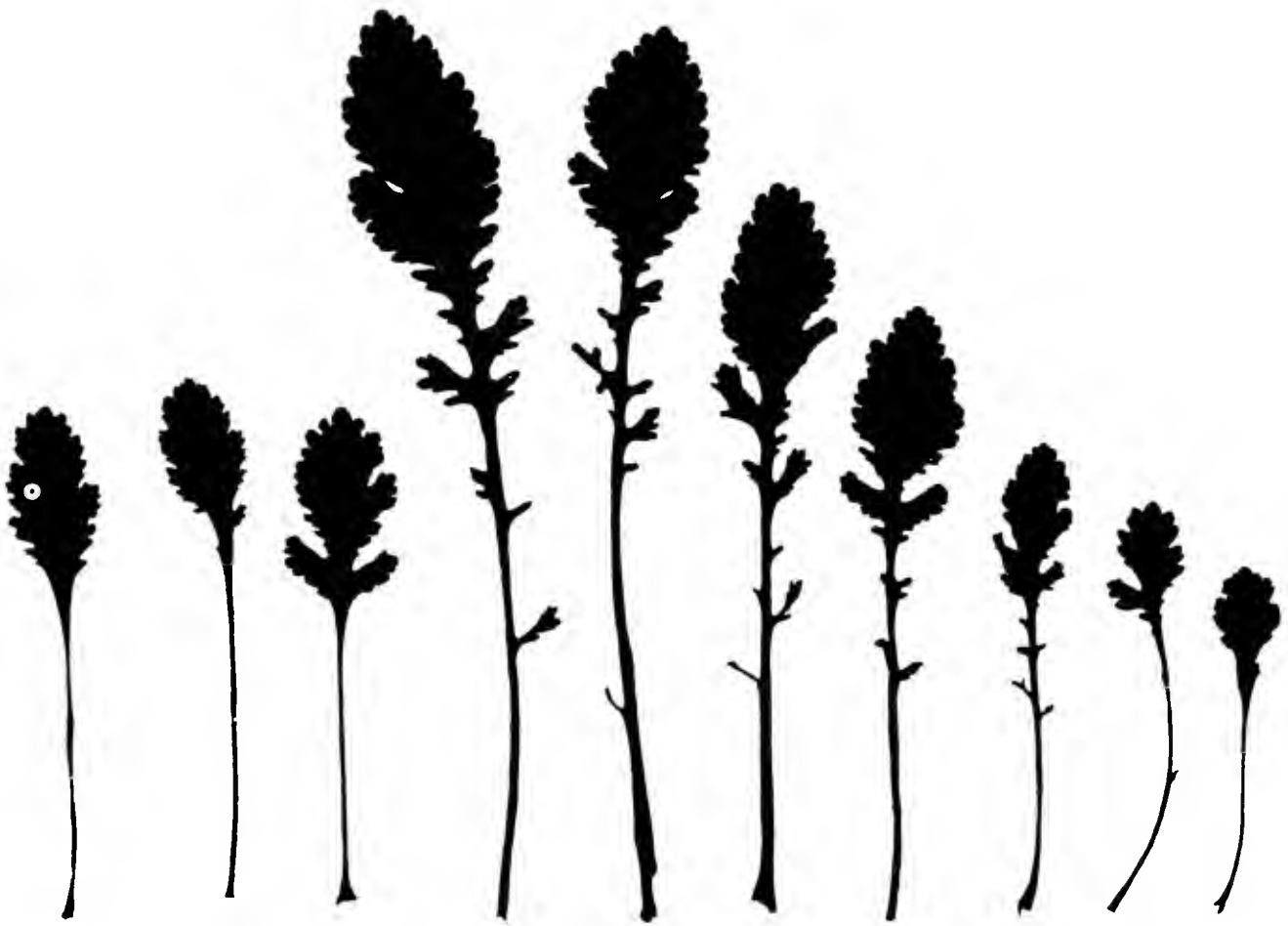


Fig. 3. Leaves of rosette and stem in *Leucanthemum praecox*.

The representatives of these species show a considerable cytological, morphological, ecological and phytogeographical diversity. However, according to their related characteristics, they may be divided into two groups. The first group includes the following four species: *L. praecox* Horvatić, $2n = (2x) = 18$; *L. vulgare* s.s Lam., $2n = (4x) = 36$; *L. rohlena* Horvatić, $2n = (4x) = 36$, $(6x) = 54$; and *L. leucolepis* Briq. et Cav., $2n = (4x) = 36$, $(6x) = 54$. Certain morphological characteristics are important for this group as for instance: branched stem, usually hairy stem and leaves; soft, wide leaves with enlarged base, edges deeply toothed in *L. praecox* (Fig. 3) and *L. rohlena*, and slightly toothed in *L. vulgare* (Fig. 4). The pappus is completely undeveloped. In *L. praecox* and *L. vulgare* the involucre bracts have dark edges and in *L. rohlena* and *L. leucolepis* light ones.

The representatives of these species are perennials flowering already in the first year. Sexual reproduction is predominant. The populations occur in habitats influenced by man, e.g. abandoned semi-cultivated fields and road edges, and rarely on pastures and meadows.

The second group of species (Fig. 1) consists of high polyploids: octoploids (*L. heterophyllum*, *L. liburnicum* and *L. illyricum*) and hexaploids (*L. croaticum* and *L. chloroticum*), occurring in the coastal region at a low altitude and on seaside mountains, as well as on inland mountains. All species of this group are perennials flowering not before the second or third year. Apart from sexual reproduction, vegetative



Fig. 4. Leaves of stem in *Leucanthemum vulgare*.

reproduction is very frequent. The habitats of their populations are mainly untouched: limestone cracks in the alpine zone above the wood border and rocky mountain pastures. Their common morphological characteristics are: unbranched stem, smooth and leathery leaves and stem, narrow leaves, pinnate (Figs. 5 and 6) or narrowly linear; and achenes of ray florets always having the pappus in the form of a membranous rim. The edges of the involucral bracts are darker in *L. heterophyllum* and to a certain extent in *L. illyricum* and *L. liburnicum*, and lighter in *L. croaticum* and *L. chloroticum*.

L. heterophyllum (Willd.) occurs in high mountains above 1000 m in the north-western part of Yugoslavia, its individuals are octoploids sometimes with 1–2 B chromosomes and very often aneuploids as well.

The other 4 species are coastal endemic species: *L. liburnicum*, *L. croaticum*, *L. illyricum* and *L. chloroticum* (Fig. 7). These were separated from the complex central European species *L. atratum* Jacq. where they were treated as subspecies. Although having many common characteristics, the representatives of the four species, studied from natural populations, display a considerable cytological, morphological

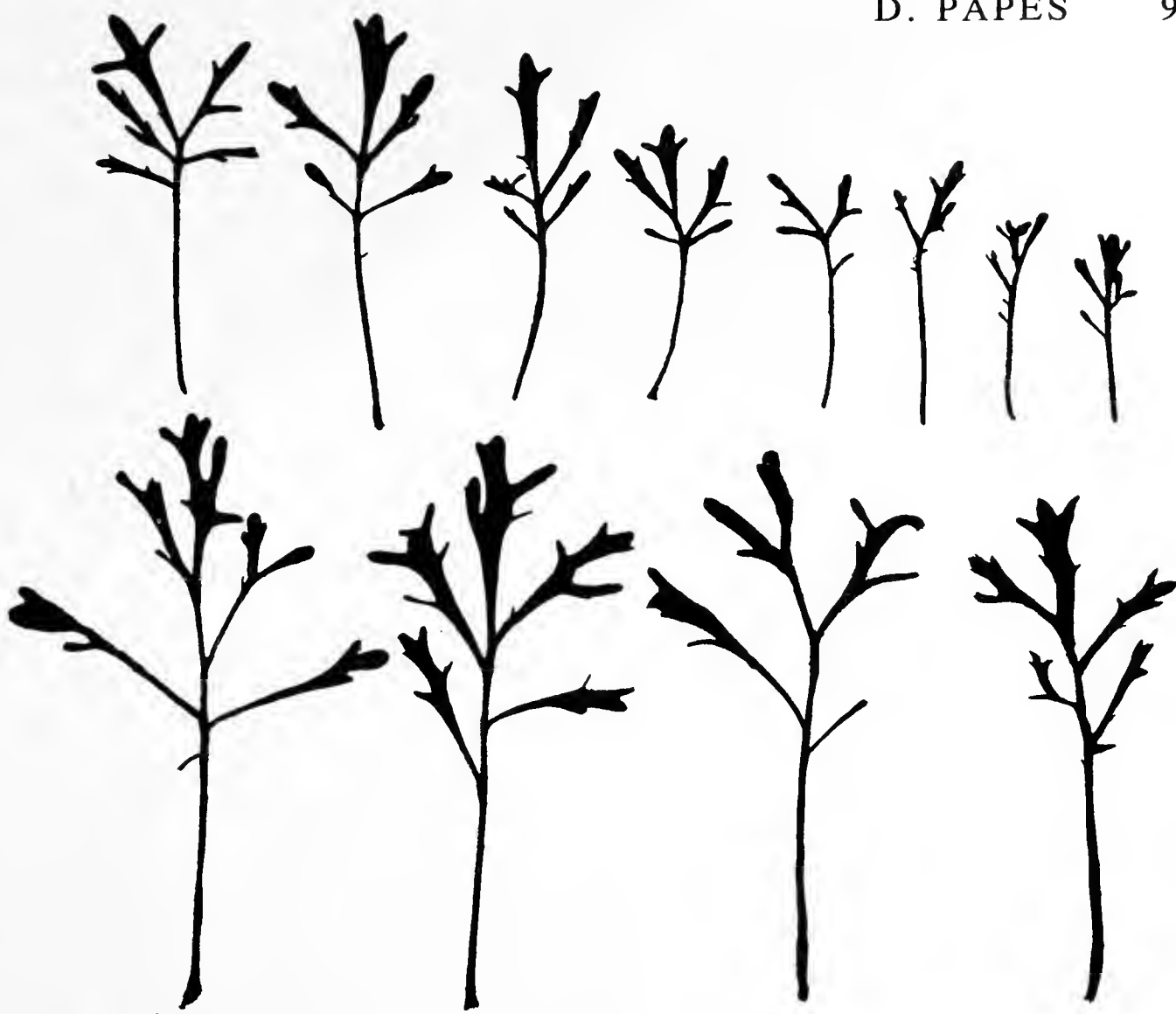


Fig. 5. Leaves of rosette and stem in *Leucanthemum croaticum*.



Fig. 6. Leaves of rosette and stem in *Leucanthemum illyricum*.

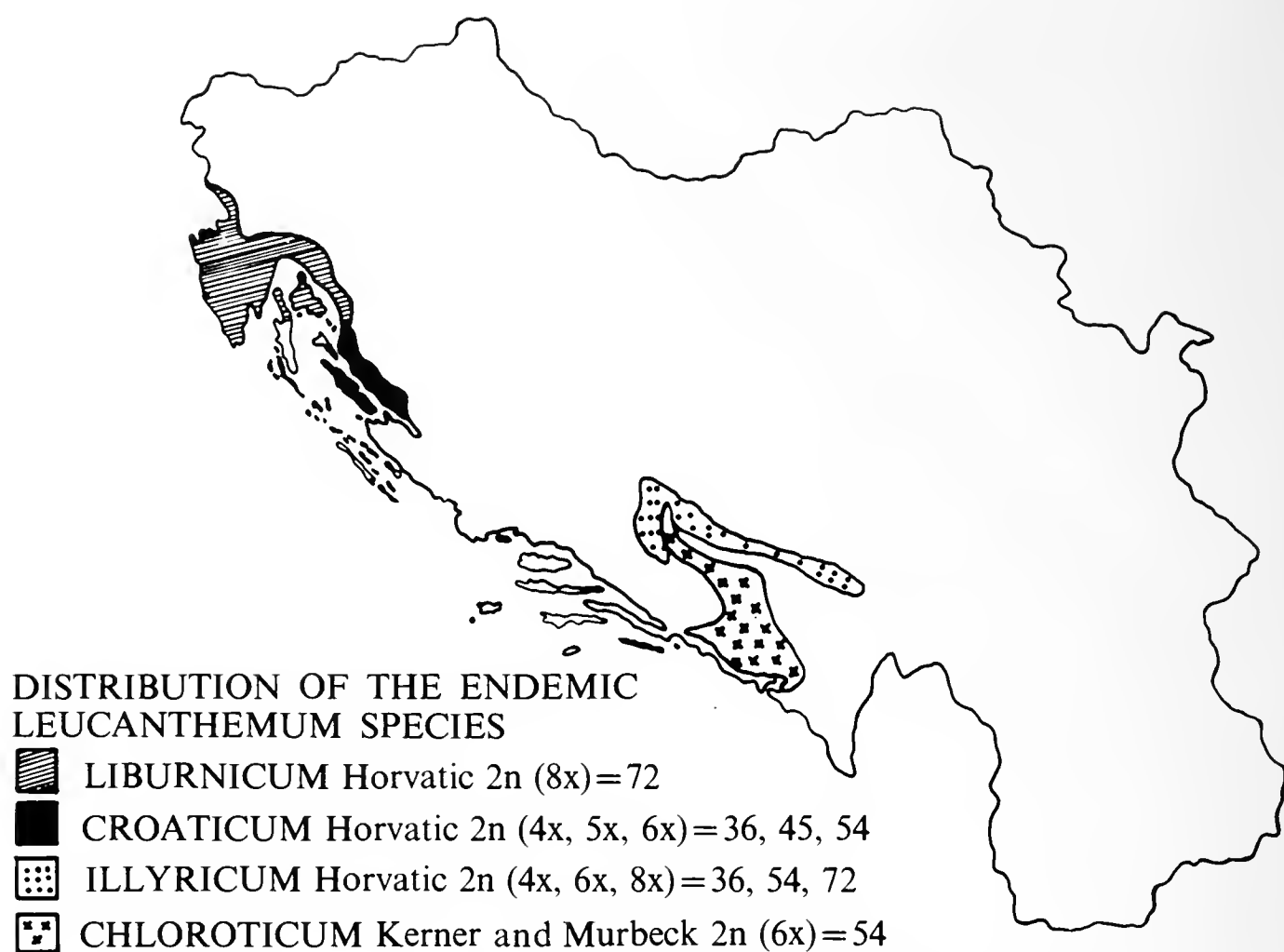


Fig. 7. Distribution of four coastal endemic *Leucanthemum* species.



Fig. 8. Leaves of rosette and stem in *Leucanthemum amplifolium*.

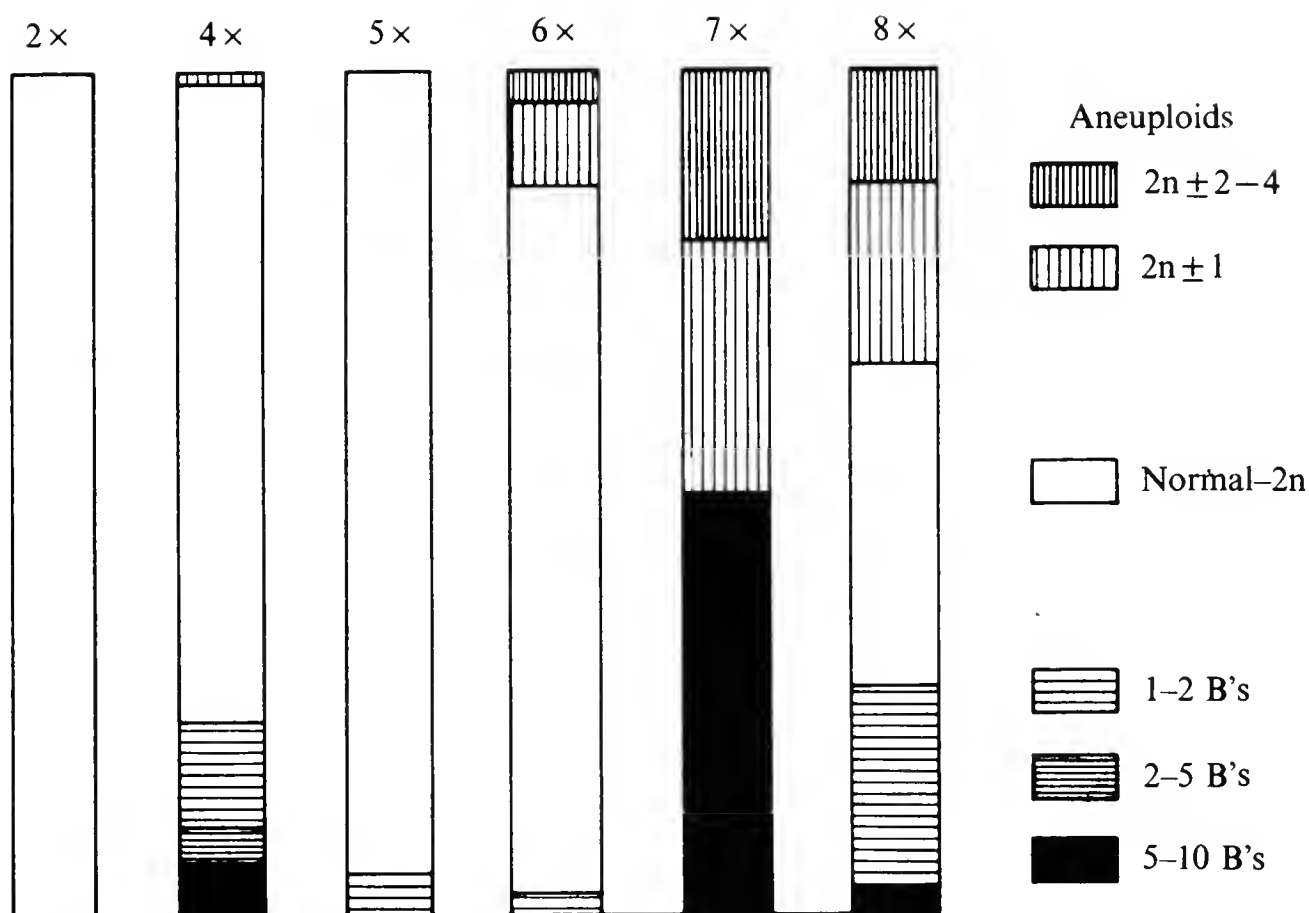


Fig. 9. Frequency of aneuploids and B chromosomes of the *Leucanthemum* species in Yugoslavia.

and geographical diversity. They are polyploids and often aneuploids, gaining and losing 1-3 chromosomes and some of them having B chromosomes. Their geographical distribution is shown in Fig. 7: *L. liburnicum* grows in the northern part of the Adriatic, *L. croaticum* occurs at all altitudes up to 1100 m above sea level, *L. illyricum* on the high mountains in Hercegovina and *L. chloroticum* on the mountains of Montenegro.

L. liburnicum Horvatić; from 6 populations were octoploids or aneuploids with $2n = 69, 70, 72, 73$ and $74+1-3$ B.

L. croaticum Horvatić (Fig. 5); in 7 populations the plants were usually hexaploids ($2n = (6x) = 54$) but some of them were pentaploids ($2n = (5x) = 45$) and a few tetraploids ($2n = (4x) = 36$).

L. illyricum (Horvatić) Papeš (Fig. 6) was usually octoploid ($2n = (8x) = 72$) and only some of them were tetraploids.

L. chloroticum Kerner et Murbeck; the chromosome numbers of its populations are $2n = (6x) = 53, 54$ and 55 .

L. amplifolium (Fiori) Papeš, $2n = (6x) = 54$ and $2n = (5x) = 45$ (Fig. 8) is an interesting species, which could represent a typical interspecific hybrid between the species of the above mentioned two groups. The most favourable parental characteristics have been crossed here, so that the newly formed species was able to survive in new habitats such as forest borders and woodland clearings.

The results of this paper show that aneuploids are very frequent and that they occur only in high polyploids (Fig. 9). It has been stated that the percentage of aneuploids grows with higher levels of polyploidy. There are no deviations in the chromosome numbers in diploids. In tetraploids they only occurred in one sample, whereas more than 30 per cent of hexaploids, heptaploids and octoploids were aneuploids.

The presence of B chromosomes was found in 11 populations out of 99 (Fig. 9). Their number varied from 1 to 10, depending on the species, the ploidy level and the method of reproduction in the population. B chromosomes were found in polyploids at all ploidy levels (4x, 5x, 6x, 8x), but they have never been found in diploids. Although in many genera the B chromosomes are a feature of diploids and are thus rarer in polyploids, in *Leucanthemum* the reverse appears to be the case. Their morphology varies at different ploidy levels, from population to population. There are three types of B chromosomes: small metacentrics in the tetraploid *L. vulgare* 1–6 Bs, and in the heptaploid (hybrid), very small metacentrics in the octoploid *L. illyricum* and telocentrics or nearly telocentrics in *L. liburnicum* (Papeš, 1971 b).

Now, if we want to say something about the evolutionary aspects of the 11 native *Leucanthemum* species from Yugoslavia, we need to look again at the diagram of possible origins and relationships of their karyotypes, where morphological features have been considered in conjunction with chromosome numbers, satellite form and frequency (Fig. 1). Only two species are diploids: *L. rotundifolium* and *L. praecox*. *L. rotundifolium* (Fig. 2) is completely isolated from the others, no other species having developed from this. *L. praecox* (Fig. 3) could be one of the parental diploid species, since its three pairs of satellited chromosomes occur also in the karyotypes of the species *L. vulgare*, *L. rohlenae* and *L. leucolepis*. However, there should still exist some diploid ancestors with at least two different characteristics, namely four submetacentric chromosomes bearing distal satellites on the short arm, and pale involucre bracts. *L. praecox* was able to survive as a diploid in seasonal isolation, flowering early in spring before the others.

The second group of species consists of high polyploids, so it is possible to assume that the ancestors of these species originated from outside Yugoslavia and should be searched for among the diploids of the Central and Southern Alps and south-western Europe, but they may even have originated from North Africa and western Asia.

As for the four endemic species, considering other authors (Contandriopoulos, 1964; Favarger & Villard, 1965; Guinochet & Logeais, 1962; Polatschek, 1966 and Villard, 1970), we have found that they are

very closely related to the *Leucanthemum* representatives in Europe, especially in the Mediterranean region, as is shown in the following:

L. liburnicum Horvatić appears as an octoploid and its allies are *L. halleri* (Sut.) Polatschek 2x, *L. atratum* (Jacq.) DC. 2x, 6x and *L. coronopifolium* Vill. 6x from the Alps.

L. croaticum Horvatić is hexaploid and, regarding morphology of leaves, its allied species extend far into western Europe and even into North Africa, these being *L. hosmariense* Ball. 2x, *L. cebennense* DC. 4x, *L. monspeliense* (L.) 4x, *L. corsicum* DC. 4x and *L. ceratophylloides* (All.) 6x.

L. illyricum (Horvatić) Papeš is octoploid and its relatives grow in the south of the Apennine peninsula.

L. chloroticum Kerner et Murbeck is hexaploid and its allies are: *L. graminifolium* Lam. and *L. Burnatii* Briq. et Cav., which are diploids, and *L. tridactylites* Kerner et Hunter which could be tetraploid.

The fact that so many polyploid-endemic species have been found may indicate that, in the evolution of *Leucanthemum* species, numerical changes are more important than structural changes.

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HYBRIDIZATION IN YELLOW-FLOWERED EUROPEAN *RORIPPA* SPECIES

B. Jonsell

ABSTRACT

The hybridization of three species of *Rorippa* in Europe is considered from the cytogenetic and the ecological points of view, and the situations seen in wild populations are tentatively explained. The role of man in extending the habitats available for vegetatively vigorous hybrid clones is estimated especially for wild lake-shore populations in Sweden.

INTRODUCTION

Rorippa, a genus of world-wide distribution, numbers approximately 80 species, most of which belong to the yellow-flowered section *Rorippa*. Three European species of this section, all long-lived perennials and pronounced outbreeders, contribute in particular to hybridization in the genus, viz. *R. amphibia* (L.) Bess. and *R. sylvestris* (L.) Bess., both widespread in much of Europe, and the eastern *R. austriaca* (Cr.) Bess. (map in Meusel, Jäger & Weinert, 1965; cf. also Jonsell, 1973), a rare alien in Britain and Scandinavia. Also *R. palustris* (L.) Bess., a short-lived perennial and highly autogamous species, may be involved in hybrids, though nearly always in highly sterile F_1 stages. In particular cases, however, a concealed, but more far-reaching role of this species cannot be excluded (see below). I will here consider mainly the interactions between *R. amphibia* and *R. sylvestris*, to some extent those between the latter and *R. austriaca*, and only touch on *R. palustris* in passing. Between the three first-mentioned hybridization has for a long time been observed, and it is well documented in herbaria. Whole series of hybrid derivatives bridging the morphological gaps between these species are present, and there are local areas where considerable fusion between them has occurred. This is particularly evident in some river systems of Central and Eastern Europe, where all three species grow together. My own experiments and field studies were based upon material from Northern and Western Europe, where the hybrid situations are more clear-cut. Fig. 1 surveys a few characters of the species involved and gives examples of some hybrid derivatives.

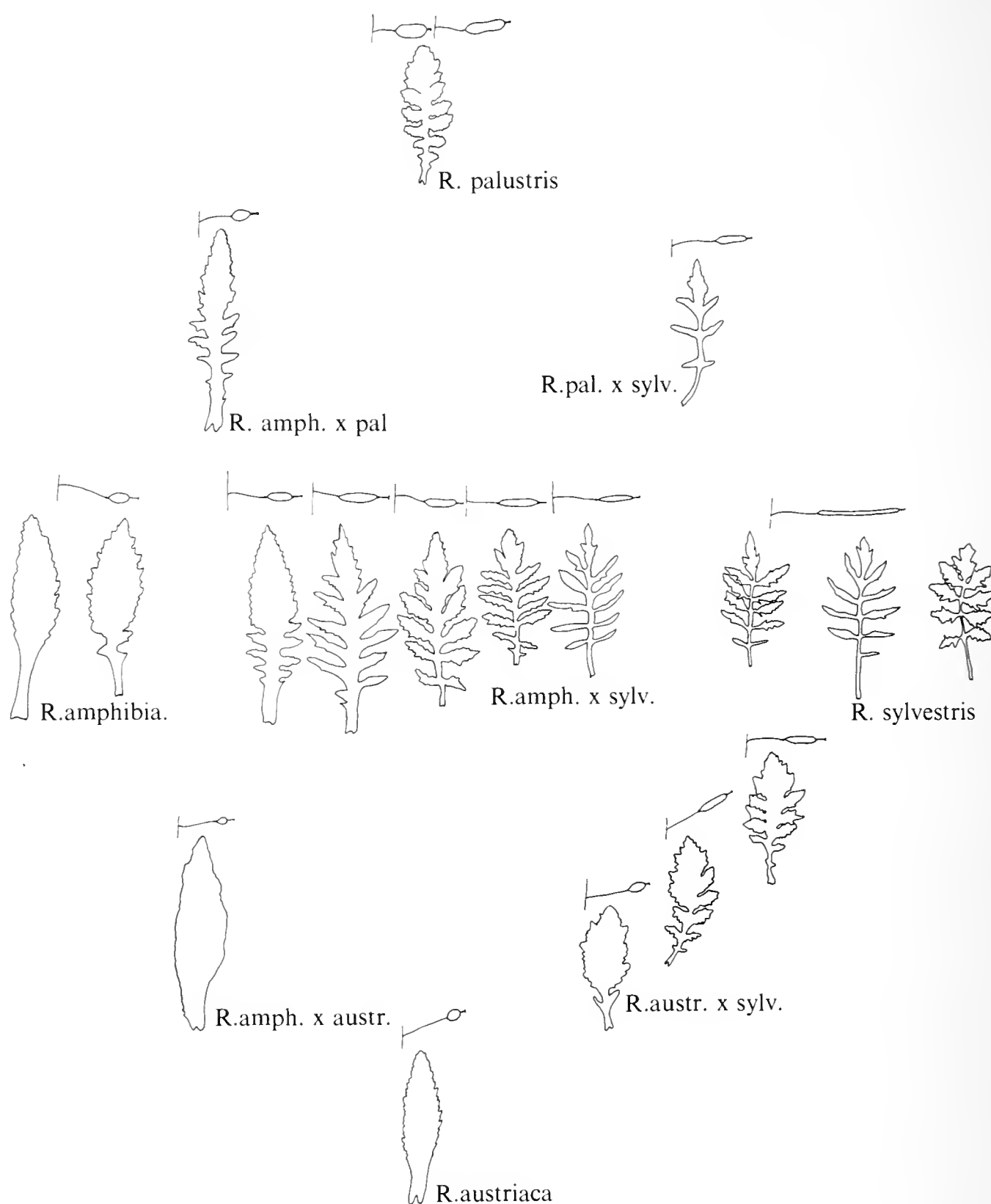


Fig. 1. Schematic survey of median cauline leaves and ripening fruits with their pedicels in some *Rorippa* species and their hybrids. According to the amount of variation one or more examples are illustrated from each species or hybrid.

POLYPLOIDY AND CROSSING ABILITY

It should first be emphasized that we are dealing with a polyploid complex, and that hybridization of significance takes place only at tetraploid or higher levels. Fig. 2 illustrates the ploidy situation and the ways in which hybrids are known to be formed in nature. For example, *R. amphibia* is in Britain both diploid (e.g. the Thames population) and tetraploid (Jonsell, 1968, p. 104); in Northern Europe only the latter.

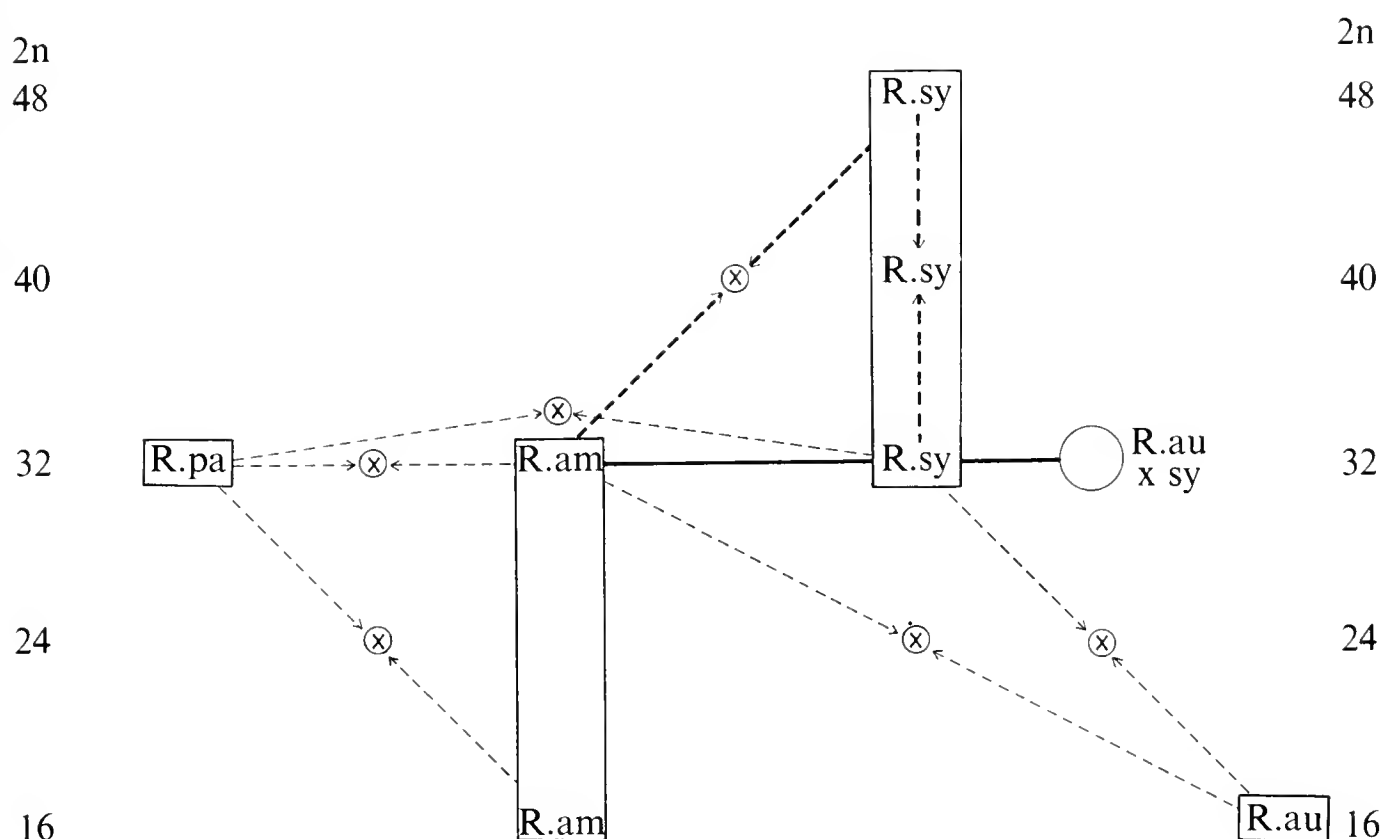


Fig. 2. Survey of polyploidy levels ($x = 8$) and spontaneous hybrid formation in hybridizing species of *Rorippa* sect. *Rorippa*. Along unbroken lines hybrid swarms occur; bold hatched lines indicate formation of fertile intermediates; thin hatched lines formation of nearly or totally sterile intermediates. See further in text.

R. sylvestris occurs frequently both as tetraploids and as hexaploids, both cytotypes apparently being widespread in Europe, at least in the north and west (Jonsell, 1968). The tetra- and hexaploid cytotypes mentioned are all actively hybridizing, which thus partly leads to the formation of pentaploids. *R. austriaca* is known as a diploid only, which offers a problem as to the way in which tetraploid *R. austriaca* × *sylvestris*, important in large parts of Europe, is formed. The mathematically possible genesis from *R. austriaca* ($2n = 16$) × *R. sylvestris* ($2n = 48$) seems less probable as the exclusive or more important way, both for morphological reasons and from the fact that we have practically unbroken series of highly fertile hybrid derivatives from one species to the other. Moreover, crosses attempted between these cytotypes failed completely (Fig. 3). Unreduced *R. austriaca* gametes may instead play an important role.

Diploid *R. amphibia* and *R. austriaca* sometimes form hybrids with tetraploids (cf. also Javůrková-Kratochvílová & Tomšovic, 1972). The resulting triploids might gain local importance, but owing to sterility, both male and female, they seem to be evolutionary 'dead ends'. Another triploid is the hybrid between *R. amphibia* ($2n = 16$) and *R. palustris* ($2n = 32$), well represented in British herbaria from the

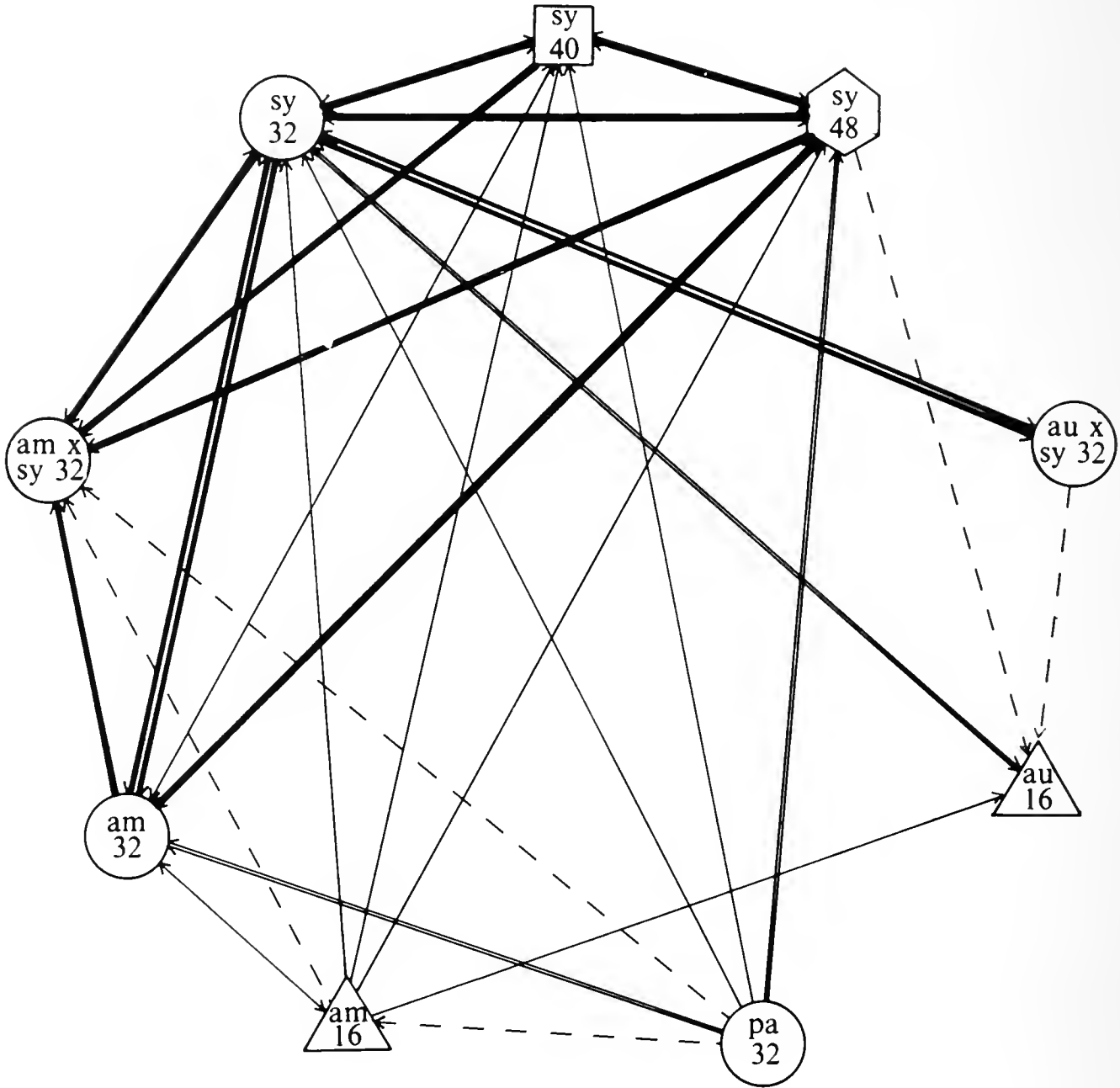


Fig. 3. Crossing polygon indicating maximum pollen fertility in F_1 -products of each combination. Hatched line = crossing failed; thin line = no progeny reaching flower; double thin line = pollen fertility in no case over 30 per cent; bold line = ditto in no case over 80 per cent; double bold line = ditto largely over 80 per cent. The polygon is mainly based on the experiments reviewed in Jonsell, 1968, pp. 42-3.

Thames banks around Kew, where it spread vegetatively. It was examined cytologically by Howard (1947).

Let us now turn from the situation in natural populations to the information about their potential to form hybrids provided by crossing experiments. The crossing polygon (Fig. 3) illustrates the pollen fertility of F_1 s obtained from wild plants; the hybrids included are also of wild origin. The progeny from each combination are, of course, varyingly fertile; in the polygon the maximum fertility observed in any derivative is shown in order to present an idea of the best that can be expected of that combination. The crossing ability is, as far as the outbreeding species are concerned, in general high at the tetraploid level, both

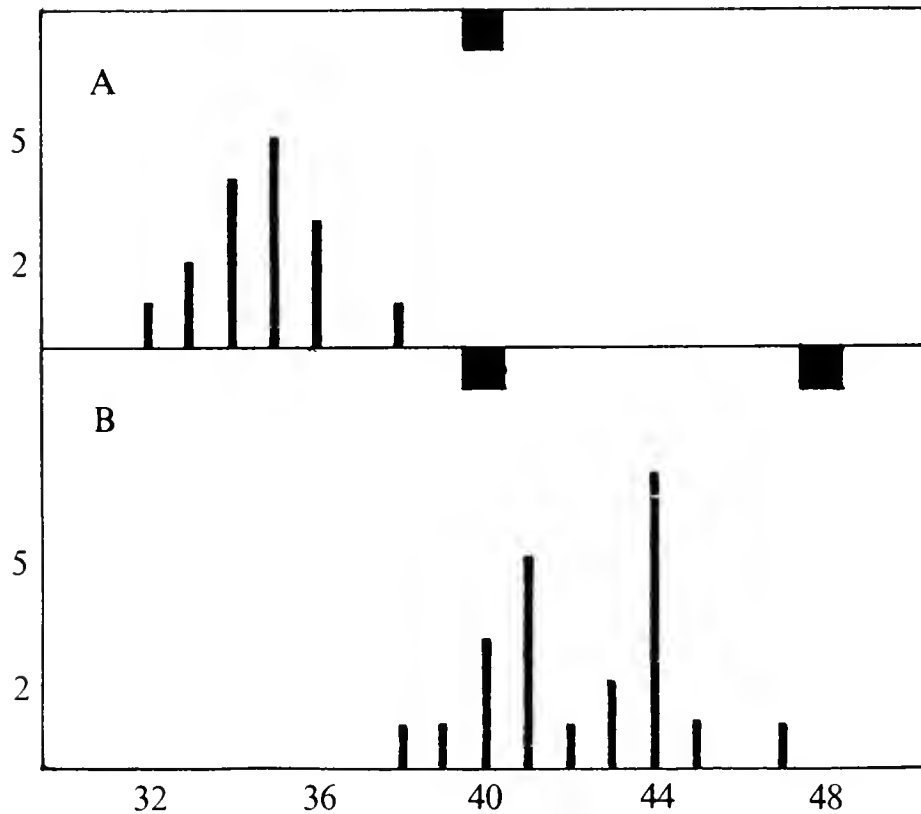


Fig. 4. Survey of two cases with aneuploid progeny raised in cultivation. (Number of individuals is plotted against somatic chromosome number; the black squares indicate chromosome number of parent plants.) A. Progeny raised from spontaneous seeds of a pentaploid *R. amphibia* × *sylvestris* hybrid, apparently back-crossed to tetraploid *R. amphibia*. B. Progeny raised from reciprocal crossings between pentaploid and hexaploid *R. sylvestris*.

between species and in back-crosses to wild hybrids. Crosses between tetra- and hexaploids were performed with about equal facility, and the pentaploids, too, can show good crossing abilities, yielding vegetatively vigorous progeny with various aneuploid chromosome numbers (Fig. 4B).

Crosses involving *R. palustris* or any of the diploids gave much poorer results, both those between various diploids and those between a diploid and some other level. Remarkable is the facility of tetraploid *R. amphibia* to cross with others at the same or higher levels, in contrast to the fact that crosses between the two *R. amphibia* cytotypes failed to give viable progeny.

Above the diploid level genetical isolation between the outbreeding species is apparently not very effective. But had these plants to rely totally or essentially upon their seeds for reproduction and dispersal, the isolation would certainly be effective enough to reduce the formation of hybrids to short-lived events without major consequences for the population structures.

DISPERSAL AND ESTABLISHMENT

The genesis of hybrids in nature is greatly favoured by both the self-sterility and the clonal behaviour of the three species, *R. amphibia*, *R. austriaca* and *R. sylvestris*. The self-sterility is very pronounced, as a rule absolute (Jonsell, 1968, p. 35). They have all, in partly different ways, effective means of vegetative propagation and dispersal. *R. amphibia* spreads by fragments of basal parts of its shoots, *R. austriaca* and *R. sylvestris* especially by portions of root-runners able to produce adventitious shoots. Local populations often consist of only a single long-lived clone. The presence in such an area of another of these species implies a very high possibility that hybrid seeds will be formed. Once a hybrid has become established, the chances for back-crossing and resulting hybrid swarms are considerable. The hybrids spread by their seeds and by shoot or root fragments. By the latter a successful hybrid derivative may build up a locally important, dominant or even exclusive population. Except for cases of anthropochory, vegetative dispersal would on the whole imply confinement to one river system. The hybrid seeds, however, may be spread over long distances, perhaps as a rule unintentionally by man, as is remarkably evident in the case of *R. austriaca* × *sylvestris* (cf. below). Another example is the almost simultaneous discovery of *R. amphibia* and its hybrid with *R. sylvestris* in a place on the River Torne in northern Finland, very far from any previously known locality of the species involved (Hylander, 1960, 1961; Jonsell, 1968, p. 130). The agency that was here responsible for the probable seed transport can, of course, only be guessed at.

Weak genetic barriers in combination with pronounced self-sterility and the ability to build up long-lived clones constitute the basic conditions for successful hybridization. But there would still be no success without suitable habitats for the hybrid products. The ecological conditions are of utmost importance for the establishment of the hybrids, a crucial point being the chances for seedlings to grow up among competing vegetation.

Let us first deal with the *R. amphibia* × *sylvestris* hybrids and briefly compare the ecological requirements of the parent species. *R. amphibia* colonizes open but rather sheltered shores and forms eventually mostly large clumps, pure or mixed up with other species, but at any rate a rather closed community. It nearly always grows in very wet places, most often with the basal parts submerged. *R. sylvestris*, when a shore plant, is bound to gravelly or sandy shores above the water level, and is much more susceptible to competition, not remaining long where the vegetation becomes dense. These two shore species have in fact very different ecological demands.

To illustrate the establishment of hybrids I will take two examples from Sweden. At Lake Mälaren (east central Sweden) the natural localities of *R. sylvestris* are the shores of a number of large eskers, formed by the retreating land-ice, that cross the lake and supply considerable stretches of rather exposed, open gravelly shores. On such places most hybrids are also to be found (cf. map in Jonsell, 1968, p. 117), sometimes a single clone only, sometimes real hybrid swarms, although the number of biotypes in one locality always seems to be rather restricted. This shows that only a very small proportion of the hybrid seeds produced gives rise to mature plants. Samples of wild hybrid seeds give rise in cultivation to many odd, but vegetatively vigorous, hybrid plants, the counterparts of which are never met with in nature (Jonsell, 1968, fig. 17, p. 119; cf. also Gorenflot, 1964, on *Plantago*). The *R. amphibia* × *sylvestris* hybrids have, as expected, in varying degree the root-runners of *R. sylvestris*, and the more they have, the more they are capable of invading the special habitats of that species, while the *R. amphibia* type of habitat is not suitable for seedlings sensitive to competition. Most hybrids established are close to F₁s between the species or to products of back-crosses to *R. sylvestris*, while those closer to *R. amphibia* seem to have greater difficulties in obtaining a foothold.

Obviously hybrids can become established under the natural conditions supplied by certain shores at Lake Mälaren. Human actions (clearings, etc.) especially formerly favoured the chances of the hybrids (e.g. swarms at small harbours outside the esker areas), but now mostly reduce them by allowing competing vegetation. The present conditions at Lake Mälaren have not prevailed for much more than 1,000 years. Earlier that stretch of water was a bay of the Baltic, probably too saline for any of the parent species. It should be emphasized that these hybrids never behave as real weeds, and the same is true for the tetraploid *R. sylvestris* of the Mälar region. Weed clones of that species are always hexaploid there, and do not invade the shores.

Hexaploid, and to a large extent also tetraploid, *R. sylvestris* consists of numerous clones which have apparently originated in connection with human cultivation, and they are, at least in N.W. Europe, neophytes when they grow on shores. In that position also the hexaploids may, when sandy or gravelly open shores are available, hybridize with *R. amphibia*, with vigorous and often rather fertile pentaploids as the result. An example will be taken from Scania (southernmost Sweden), a lake with sandy shores recently formed by lowering of the water level. One hexaploid *R. sylvestris* clone invaded the shores and crossed with the indigenous tetraploid *R. amphibia* forming a commonly occurring pentaploid hybrid, vigorous and highly fertile. In spite of

careful investigations no aneuploid back-cross products were found in that place, but spontaneous seeds from the pentaploids gave rise to aneuploid progeny (Fig. 4A), easy to raise and keep in cultivation, but obviously incapable of becoming established in nature. Spontaneous aneuploids are on the whole unknown in this clonal complex and unlike many others (e.g. *Cardamine pratensis*, Lövkvist, 1956; *Achillea*, Ehrendorfer, 1959) it seems to show an obstacle to fusion between the polyploidy levels. In this example human action has clearly been the condition for the establishment of the hybrids, but not even here do they spread as weeds. Situations ecologically similar to the Scania example, with rather intermediate pentaploids and or with tetraploid hybrid swarms, seem to prevail in N.W. Europe.

The *R. austriaca* × *sylvestris* hybrids have quite other ecological requirements. Like both parent species they have root-runners and they are as well as any of them able to inhabit dry places in the cultivated landscape (harbours, roadsides, railways, gardens, etc.). They are in N.W. Europe totally dependent on human cultivation and appear everywhere as weeds. They occur far outside the range of native and even introduced *R. austriaca*, forming independent long-lived clones, which have slight chances of seed-setting and thus contributing to the origin of new genotypes. They might exceptionally meet tetraploid *R. sylvestris*, but where new genotypes appear, fresh introductions of hybrid seeds as a rule seem to have occurred. In Sweden, seeds formerly arrived with cereals imported from the Black Sea region, where the hybrid is frequent (Jonsell, 1973), but other ways of introduction have certainly occurred (Jonsell, 1968, p. 143). Perhaps into Sweden, but in any case within the country, the root-runners are transported by soil, just as weed clones of *R. sylvestris*, and the hybrid is now in some places a prominent garden weed. In British herbarium material not a single specimen of this characteristic hybrid was found.

INTROGRESSION

The very variable tetraploid *R. sylvestris* shows in many areas features of *R. amphibia* in spite of the absence of intermediate plants, sometimes in single individuals, sometimes in whole local populations (e.g. in Britain, along the River Severn and River Wye in Monmouthshire). Introgression has obviously occurred on the tetraploid level via now extinct or very rare hybrids. To return to the area of Lake Mälaren in Sweden, it is striking that the comparatively rare *R. sylvestris* is there very variable with many local, characteristic clones, while the much more numerous and widely distributed *R. amphibia* is highly uniform.

R. sylvestris seems practically everywhere by this lake to be influenced by hybrid processes, while *R. amphibia* is largely left untouched. This may be explained by considering its nearly always much larger populations, where a few introduced genes will be merely swamped, as well as the difficulties for seedlings to become established in them. *R. palustris* grows in the area, too, and it cannot be excluded (though it is very difficult to prove) that it has not in some degree contributed to the variability of *R. sylvestris*. No intermediates between them are known, but it is obvious that only those derivatives which have the effective root-runners of *R. sylvestris*, and consequently as a rule are close to that species in other respects as well, would have chances in the long run.

CONCLUSIONS

We have seen here that habitats free from competition are necessary for the establishment of *R. amphibia* × *sylvestris* hybrids, and that these conditions can be supplied under natural circumstances, but are more often the consequences of human action. The ecological restrictions of these hybrids, going back to the diversity in life history of the parent species, put limits on the hybrid process, the more so since these hybrids (but not *R. austriaca* × *sylvestris*) seem incapable of fully utilizing the advantages supplied by man to become weeds.

Although the hybrid nature, or at least the intermediate character, of all the actual forms has been evident from their discovery, they have taxonomically often been treated as species. This is still the case in Central Europe for '*R. prostrata* (Berg.) Schinz & Thell.', a name that stands for *R. amphibia* × *sylvestris* which is probably in the form of both pentaploids, comparatively clear-cut and often independent, and less clear-cut tetraploids. The local clones, similar from one river system to the other, give the impression of constituting a species, but no evidence to hand speaks in favour of such an interpretation.

Broadly seen there are many counterparts in other genera to the hybrid situation met with in the yellow-flowered *Rorippas*, which fit a model with the combination of a clonal and a polyploidal complex as the significant point. The polyploidy has its consequences for the breakdown of genetic isolation, but it is also true that, of the two cytotypes of *R. amphibia*, the tetraploid has a much wider distribution to the north and east than the diploid. *R. sylvestris* s.str. is not known from below the tetraploid level, but a closely related form restricted to Hungary, *R. kernerii* Menyh. (= *R. sylvestris* ssp. *kernerii* (Menyh.) Soó) is reported to be diploid (Borsos, 1970), and there are other restricted taxa close to *R. sylvestris* in S.E. Europe and further

eastwards (Jonsell, 1973). The polyploids, which meet and hybridize, have probably to a large extent thanks to civilization reached their present ranges, at least in N. Europe. This means that Man's influence may be behind it all, even where the hybrid process now seems to be going on under natural conditions.

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WILD HYBRIDS IN THE BRITISH FLORA

C. A. Stace

ABSTRACT

Hybrids have not received from British field-botanists enough of the precise and detailed attention they deserve. This is at least partly due to uncertainties regarding the number, characteristics and abundance of hybrid combinations which exist. Such information, as far as it is known, has now been made generally available in a book, *Hybridization and the Flora of the British Isles*, published in 1975. The text was prepared by 86 experts over a total period (from inception to publication) of more than 6 years.

This paper presents some statistics from the book relating to the number of interspecific hybrid combinations found in the British Isles. A total of 975 such hybrids are included, of which 626 are reckoned to be well substantiated, 122 possibly correctly recorded, and 227 erroneously recorded or probably so. Possible reasons for the varying abundance or patchy distribution of many hybrids are discussed, with particular reference to those found on the Continent of Europe but not in the British Isles.

INTRODUCTION

The study of hybrids and hybridization between distinct species of plants has a long, involved and often controversial history, the earlier phases of which are documented and discussed in two excellent textbooks (Roberts, 1929; Zirkle, 1935). Aspects which are even today still in contention include factors involved in the formation and establishment of hybrids; the abundance, distribution and ecological importance of hybrids in the wild; and the overall evolutionary significance of hybridization. In this paper I hope to present some facts which may go a little way towards answering just two of these points: how common are hybrids in the wild, and what factors determine their frequency?

It is important to be able to answer these questions because they are basic to all the others; it is clearly not possible to estimate the importance or significance of a phenomenon if one does not know how common it is. At a more practical level the accurate recognition and

recording of hybrids is essential to field-botanists, not only because of the intrinsic interest of hybrids, but also because such information will reveal the exact limits of the parents in terms of both structural variation and distribution. This is obviously a two-way process, because it is inevitably the field-botanists who are going to produce most of the primary data on variation and distribution.

The absence of sufficient primary data has in the past often led to a subjective view of hybridization being adopted by botanists, who have in many cases become either 'believers' or 'non-believers'. But, just as with those other two opposing groups, the 'splitters' and 'lumpers', constant adherence to one dogma will prove to be as often misguided as judicious. It is perhaps not too obvious to emphasize that each case must be judged on its own particular evidence, and that the gathering of such evidence is an essential preliminary to sensible judgement.

Nevertheless, the possibility that hybrids exist has often provided a sort of escape clause in taxonomically difficult groups. If two taxa are separable only with difficulty the presence of troublesome intermediates can all too easily be ascribed to hybridization. If little is known of the group, and experimental studies have not been carried out, it might be impossible to know whether or not this is the correct interpretation. There is a great number of records of hybrids in this category. Many of them have since been confirmed or refuted, but others remain uncertain.

The existence of so much uncertainty, and the widely scattered sources of reliable information, much of which is unpublished, prompted the proposal by Professor D. H. Valentine and Dr S. M. Walters in 1968 (following a suggestion by the former in 1950), that a book should be compiled to act as a source of reference concerning all that is known about British wild hybrids. The scope of the book (Stace, 1975) is limited to vascular plant hybrids reported from the wild in the British Isles, and involving two or more taxa generally differing at the species level or above. These limitations are somewhat arbitrary, but a course was chosen as close to completeness as possible without setting an unrealistic target. The limitations also set the book apart from that all-embracing classic monograph on hybrids, *Die Pflanzenmischlinge* (Focke, 1881), but of course the information now available for each hybrid is vastly more detailed and diverse than in 1881, and far more hybrids are now known. *Hybridization and the Flora of the British Isles* was published in 1975 (more than six years from its inception) under my editorship, but involving 86 different authors, each with specialist knowledge in one or more genera.

The aim of the book is to lay out the evidence, both circumstantial and experimental, concerning every hybrid combination claimed to

have been found in the British Isles. This, it is hoped, will prove of value to both amateur and professional botanists in a number of ways. In particular it should provide teachers with ideas for examples and projects, enable research workers to pinpoint queries and problems, and aid field-workers in identifying hybrids more accurately and in showing up gaps in our information which they might be able to fill. Perhaps the first purpose that the book has served has been to provide some of the basic data presented in the next few paragraphs.

SOME STATISTICS

Before analysing the number of hybrids which occur or have been recorded it is important to consider the raw material available for hybridization, i.e. the number of species in the British Isles. One can never obtain an exact number because no two authors are of precisely the same opinion concerning species limits, or concerning the criteria for the inclusion of alien species, but the figures given in a modern authoritative work (Dandy, 1958) give a good idea of the situation. Dandy listed 2,179 native species, of which 610 were 'additional microspecies' in the genera *Rubus* and *Hieracium*, plus 643 naturalized alien species. One should probably add about 180 native microspecies to account for species of *Rubus* and *Hieracium* since recognized, and for the microspecies of *Taraxacum*, which were not listed by Dandy. But the total figure of 3,002 (which many workers would wish to increase substantially by the addition of further naturalized species) means little by itself, because the majority of the microspecies are agamospecies unable to hybridize, and even the figure of 2,212 for the remainder does not take into account their degree of relationship. The data in Table 1, which lists the number of species in the larger genera, are therefore relevant. They show that 35 genera contain ten or more species, but that only seven contain more than 21 species and that three of these are the large agamospermous genera previously mentioned. It should be emphasized that these figures are not taken directly from Dandy (1958), but are updated and include native species only.

Table 2 indicates that of 720 British genera almost exactly half are monotypic in the British Isles, and that almost exactly half of the remainder form no hybrids solely involving British species either in the British Isles or elsewhere. Of the remaining genera which do form hybrids, 143 form hybrids in the British Isles and a further 38 form hybrids solely involving British species but only abroad. Of course, many of the monotypic genera and of the polytypic genera which are listed as forming no hybrids do form hybrids abroad involving one or more non-British species. Good examples are *Pulsatilla*, *Elymus* and

Table 1. *Numbers of native British species in the larger genera of the British flora*

<i>Rubus</i>	c. 400	<i>Juncus</i>	26
<i>Hieracium</i>	c. 250	<i>Euphrasia</i>	26
<i>Taraxacum</i>	c. 140	<i>Ranunculus</i>	24
<i>Carex</i>	80	28 others	10-21

Table 2. *Numbers of genera in the British flora analysed according to their propensity for hybridization*

	720	genera
of which	366	are monotypic
	354	
of which	173	form no hybrids
	181	
of which	38	form hybrids abroad
leaving	143	which form hybrids in the British Isles

Pedicularis. The figures 720 and 366 are taken direct from Dandy (1958), but the other numbers have been gathered from *Hybridization and the Flora of the British Isles*.

In addition there are 14 confirmed intergeneric hybrid combinations in the British Isles, involving both monotypic and polytypic genera, and in the latter case both those forming other hybrids and those not. These include five in the Orchidaceae and five in the Gramineae, and are listed in Table 3. Apart from many other erroneous or doubtful claims of intergeneric hybrids in the British Isles there are records of 22 additional intergeneric hybrid combinations abroad solely involving British species (e.g. in *Dactylorhiza*×*Pseudorchis*), and a further 11 combinations of British genera where one or both of the species involved are non-British (e.g. in *Cotoneaster*×*Sorbus*). Naturally, whether a hybrid is intergeneric or not depends entirely upon one's concept of the limits of the genera concerned, and it is true that several of the combinations in Table 3 would not be considered intergeneric by some workers. The generic limits used by Dandy (1958) have been employed for the present purpose.

Table 4 gives the total number (975) of interspecific (including intergeneric) hybrids recorded from the British Isles, and attempts to

Table 3. *Intergeneric hybrid combinations in the British flora and the number of specific combinations in each. Data taken from Stace (1975)*

	Nos. of hybrids
<i>Asplenium</i> × <i>Phyllitis</i>	3
<i>Crataegus</i> × <i>Mespilus</i>	1
<i>Conyza</i> × <i>Erigeron</i>	1
<i>Anthemis</i> × <i>Tripleurospermum</i>	1
<i>Coeloglossum</i> × <i>Gymnadenia</i>	1
<i>Coeloglossum</i> × <i>Dactylorhiza</i>	3
<i>Gymnadenia</i> × <i>Pseudorchis</i>	1
<i>Dactylorhiza</i> × <i>Gymnadenia</i>	4
<i>Anacamptis</i> × <i>Gymnadenia</i>	1
<i>Festuca</i> × <i>Lolium</i>	6
<i>Festuca</i> × <i>Vulpia</i>	4
<i>Agropyron</i> × <i>Hordeum</i>	1
<i>Ammophila</i> × <i>Calamagrostis</i>	1
<i>Agrostis</i> × <i>Polypogon</i>	1
	<hr/> 29

Table 4. *Numbers of interspecific hybrids recorded in the British flora. Data taken from Stace (1975)*

626	confirmed or probably correct
122	possibly correct
227	erroneously recorded or probably so
<hr/> 975	
464	recorded only abroad
<hr/> 1439	

classify them into three groups according to the degree of certainty of the record. It seems likely that at least 25 per cent of the combinations are erroneously recorded. In addition there are 464 hybrids between British species which have been found abroad but not in the British Isles. These figures are taken from the new hybrid book (Stace, 1975), and easily exceed the number of hybrids mentioned in any other British work (see Stace, 1975, p. 22). However, the figure of 464 for the ‘foreign hybrids’ should be used with much caution, for it does not pretend to be complete, and it includes a proportion of records which will almost certainly turn out to be ill-based. Moreover the above figures do not include hybrids between the microspecies of *Rubus*. In this genus

Table 5. *Numbers of hybrids in the British flora in the eight most hybridogenous genera. Data taken from Stace (1975)*

<i>Salix</i>	59	<i>Carex</i>	34
<i>Euphrasia</i>	54	<i>Rumex</i>	29
<i>Epilobium</i>	48	<i>Potamogeton</i>	25
<i>Rosa</i>	37	<i>Dactylorhiza</i>	19

there are many more or less sterile hybrids known in the British Isles and elsewhere, but in addition it is likely that a very high (and quite unknown) proportion of the generally recognized microspecies are in fact hybridogenous, having become stabilized by agamospermy. Finally, the book also includes 23 intraspecific hybrids which for various reasons are given as full a treatment as the interspecific ones.

Table 5 shows the distribution of hybrids in eight genera. These possess from 19 to 59 confirmed hybrids; no other genus possesses more than 13, apart from the special case of *Rubus* mentioned above. Of the eight, *Epilobium* and *Dactylorhiza* have by far the largest number of hybrids in relation to the number of species, for almost every parental combination has been found. At the other end of the spectrum one can list ten rather large genera which form no hybrids at all: *Trifolium*, *Vicia*, *Lathyrus*, *Alchemilla*, *Sedum*, *Oenanthe*, *Orobanche*, *Campanula*, *Hieracium* sensu stricto and *Allium*. The absence of hybrids in *Alchemilla* and *Hieracium* can of course be explained on the basis of agamospermy, but in the other cases it is probable that strong interspecific incompatibility barriers do really exist, and in several of them (e.g. the three Leguminosae and *Allium*) this has been demonstrated experimentally. It is possible that *Polygonum* should be added to the above list, for none of its many reported hybrids has been satisfactorily proven.

IDENTIFICATION AND DISTRIBUTION OF HYBRIDS

It is clear from the above data that, even if the erroneous or doubtful records are ignored, a great many hybrid combinations are to be found in the British Isles. The distribution and frequency of these hybrids are, however, far less easily ascertained. Undoubtedly many hybrids are rare, but many are not and a good number are greatly under-recorded; it is to be hoped that more intensive work by field-botanists will help to fill the many gaps in our information. Perring & Sell (1968) mapped about 50 hybrids in their *Critical Supplement to the Atlas of the British Flora*, including a number of more frequent ones and others which are

easily recognized or for which reliable information had already been accumulated by specialists. That this is only about 8 per cent or perhaps less of the total number is a good illustration of the imperfect state of our knowledge.

Detailed recording of hybrids in the field naturally relies upon accurate identification, the lack of which in the past has resulted in a very large number of erroneous records. Most of these should have been referred to extreme or abnormal states of one (or both) putative parents, or to a third species. Species which have at one time been wrongly attributed to a hybrid status often bear the specific name of *hybridus* or *intermedius*, etc.

It is not possible here to provide detailed hints on the determination of hybrids, but three general points are perhaps not out of place.

(a) While most hybrids are sterile to a lesser or greater degree, sterility by itself is not a very good criterion. Many hybrids are highly or even completely fertile, and in addition hybrids which are in reality largely sterile may appear to have perfectly viable pollen (e.g. most *Juncus* hybrids). This may be due to the facts that sterility can exist mainly on the female side, or can take effect only after pollination. Moreover, the lack of good pollen and/or seed can be caused by many factors other than hybridity, for instance the lack of a compatible pollen source (e.g. *Calystegia* spp.), or environmental effects (as is common in *Juncus inflexus*).

(b) Hybrids are not always exactly or even roughly intermediate in appearance between their parents. Often some of the characters are intermediate, while others (perhaps the most conspicuous) are close to one or other parent. In other cases a hybrid may much more closely resemble one parent than the other in all characters (e.g. *Geranium purpureum* × *G. robertianum*), or may exhibit some features not found in either parent (e.g. *Papaver dubium* × *P. rhoeas*).

(c) It is dangerous to extrapolate evidence obtained from the study of one hybrid to other closely similar or related hybrids. Often, of course, a series of hybrids among a well-defined group of species has many features in common, but it is not rare to find the opposite situation. For example, the three hybrids known to involve *Juncus effusus* are, respectively, fully fertile (× *J. conglomeratus*), slightly fertile (× *J. inflexus*), or completely sterile (× *J. balticus*).

There are also often many surprises concerning the distribution of hybrids. In particular there are numerous instances where hybrids do not occur wherever the two parents co-exist, even though the latter might be highly compatible. The reasons for this are very various and in general well documented by several reviewers, and need not be gone into here. They can be placed into two main categories:

(a) The isolating barriers normally separating the two species break down in some places only. This is an obvious possibility in the case of external barriers, since many aspects of the environment vary from place to place, but is no less true of internal barriers. It is a fairly common experience to find that a hybrid not previously synthesized despite numerous attempts has been readily obtained with a new, different genetic stock of one or both parents, or vice versa.

(b) Hybrids can become established in certain areas, but not in others. This is often the result of disturbance of the habitat by man, who unwittingly creates new niches suitable for hybrids.

Of greatest interest to British botanists are those hybrids which have been found in the British Isles but not elsewhere (e.g. *Daphne laureola* × *D. mezereum*, various *Festuca* × *Vulpia* combinations), or vice versa; 464 of the latter category are mentioned in the new hybrid book. Some of these records are probably erroneous, and others represent combinations unlikely to occur in the British Isles because the parents do not come into contact (e.g. *Juncus balticus* × *J. filiformis*) or because of the rarity of one or both parents (e.g. *Aceras anthropophorum* × *Orchis simia*, *Woodsia alpina* × *W. ilvensis*). But a detailed search in this country for the others could well be rewarding; it would determine the precise pattern of hybrid distribution compared to that of the overlap of the parents, and also help to assess the factors isolating the parents as well as those causing breakdown of isolation.

The discovery of several hybrids new to the British Isles (or to science) in the past few years shows that the British list is by no means complete. Among the many hybrids known abroad and which might be found in the British Isles the following 15 have been selected from genera (or generic combinations) which have so far no known hybrids in this country:

Asplenium ruta-muraria × *Ceterach officinarum*
Cystopteris fragilis × *C. montana*
Gymnocarpium dryopteris × *G. robertianum*
Dianthus armeria × *D. deltoides*
Scleranthus annuus × *S. perennis*
Pimpinella major × *P. saxifraga*
Pyrola minor × *P. rotundifolia*
Cynoglossum germanicum × *C. officinale*
Sambucus nigra × *S. racemosa*
Aceras anthropophorum × *Herminium monorchis*
Dactylorhiza fuchsii × *Pseudorchis albida*
Aceras anthropophorum × *Orchis purpurea*
Dactylis glomerata × *D. polygama*

Melica nutans × *M. uniflora*
Phleum bertolonii × *P. pratense*

JUNCUS BALTICUS HYBRIDS

It is likely, however, that even after quite detailed analyses the explanations of many odd patterns of distribution will remain unanswered. It is often very difficult to pinpoint a particular factor involved in species isolation, and frequently it is a complex interaction of a number of isolating factors which is operating. I want to illustrate such difficulties by describing a situation in *Juncus* subgenus *Genuini* concerning certain hybrids involving *Juncus balticus*.

Juncus balticus hybridizes with *J. arcticus* in arctic and subarctic areas where the two species meet. The two species are closely related and several authors consider them to represent subspecies of a single species. In much of north-western Europe, particularly around the coasts of the Baltic, *J. balticus* meets *J. filiformis*, and these two species frequently hybridize in such situations. As mentioned above, their ranges do not overlap in the British Isles.

The other two hybrids of *J. balticus* are far less widespread, there being three valid records of each. *J. balticus* × *J. effusus* has been found in two localities on the Lancashire coastal dune-systems, and one in a similar situation on the Baltic coast of East Germany, near Ribnitz (type locality for *J. × obotritorum* Rothm.). Both of the Lancashire localities for this hybrid have been eradicated by building developments, one in 1968 and the other in 1974. The few other records for this hybrid are errors for *J. balticus* × *J. filiformis*, including the type of *J. × scalovicus* Aschers. & Graebn., which was originally attributed by Ascherson & Graebner (1893) to *J. balticus* × *J. effusus*. Finally, *J. balticus* × *J. inflexus* occurs in three localities on the Lancashire coastal dune-systems, two of them fortunately within the boundaries of nature reserves. There are morphological and/or anatomical differences between each of these six colonies of hybrid *Juncus*, all of which are completely sterile, and it seems likely that each of them is the result of a separate hybridization, five of them within a 27 km stretch of the coast of Lancashire (see map in Stace, 1972).

Fig. 1 shows the extent of the overlap of the ranges of *J. balticus*, *J. effusus* and *J. inflexus*, covering a considerable band of terrain mainly on or near Baltic and North Sea coasts, as well as the two areas in which hybrids are known to occur. The British area (Lancashire) coincides with an outlying locality for *J. balticus* (separated from others by c. 300 km), but the German area is in a part of the range where *J. balticus* is very common, albeit near its southern limit.

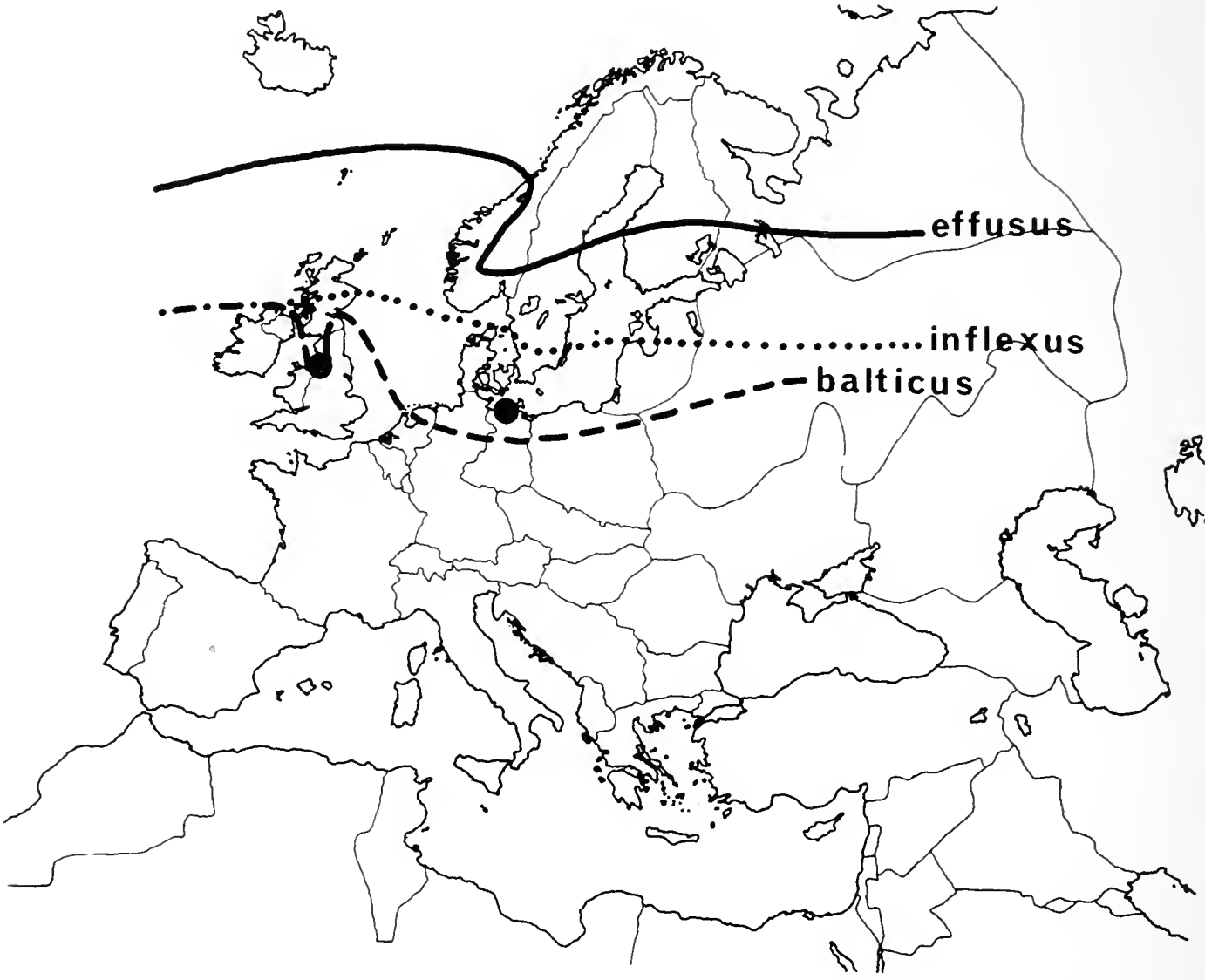


Fig. 1. Approximate northern limits of *Juncus effusus* and *Juncus inflexus* and approximate southern limit of *Juncus balticus* in Europe. The dots indicate the two localities of the six hybrid populations mentioned in the text.

Table 6. *Chromosome numbers of J. balticus, J. effusus, J. inflexus and their hybrids determined in the present study*

<i>J. balticus</i>	$2n = 84$
<i>J. effusus</i>	$2n = 40$
<i>J. inflexus</i>	$2n = 42$
<i>J. balticus</i> × <i>J. effusus</i> ‘Ainsdale’	$2n = 82$
<i>J. balticus</i> × <i>J. effusus</i> ‘Hightown’	$2n = 80-82$
<i>J. balticus</i> × <i>J. inflexus</i> ‘Fylde’	$2n = 82-84$
<i>J. balticus</i> × <i>J. inflexus</i> ‘Birkdale’	$2n = 84$
<i>J. balticus</i> × <i>J. inflexus</i> ‘Freshfield’	$2n = 84$
<i>J. effusus</i> × <i>J. inflexus</i>	$2n = 42$

The five British colonies have been examined cytologically (Table 6), and show that the *J. effusus* or *J. inflexus* parent contributed in each case an unreduced gamete. The diffuse-centric, very small (mostly 0.3–0.5 μm long) chromosomes of *Juncus* subgenus *Genuini* are very difficult to count with complete accuracy, and it is still not certain whether any species possesses more than one chromosome number, but the results obtained clearly indicate that *J. balticus* and both its hybrids have roughly twice as many chromosomes as the other two species and the hybrid between them. Many attempts have been made to re-synthesize these hybrids, using several different parental strains, including those from the Lancashire coast, but no hybrids have so far been produced. All three species are self-compatible and wind-pollinated, and usually set seed freely. One not infrequently encounters sterile colonies of *J. inflexus* (which in the following year may produce plenty of good seed), and the same has been reported for *J. balticus*, but in the years I have been studying them the Lancashire clones of *J. balticus* have always formed abundant viable seed both *in situ* and in the botanic garden.

DISCUSSION

The occurrence of five of the six known colonies of these hybrids within 27 km of each other, despite the abundant cohabitation of the parents over a wide area of northern Europe, is both intriguing and perplexing, and leads one to question what factors so conducive to hybridization might exist in Lancashire yet not elsewhere.

There are many other areas known where hybridization is a notoriously frequent phenomenon, but these generally involve hybrids over a wide taxonomic spectrum and can be related to disturbance of the habitat and to the influx of new (often weedy) species. New Zealand and Hawaii are two well-known examples. In New Zealand forest fires and clearance by man have been suggested as the major factors (see Cockayne & Allan, 1934), while in Hawaii hybridization has followed the colonization of open volcanic terrain by immigrant species (see Gillett, 1972).

Briggs & Walters (1969, p. 197) have suggested that introgression, first detected and most studied in North America, where much of the present-day vegetation is the result of man's very recent activities, might in fact be more prevalent there than in Europe, where the vegetation has had a greater chance to reach an equilibrium with man's requirements over several millennia. In the Orkneys Miss E. R. Bullard (the B.S.B.I. recorder for those islands) has informed me (*in litt.* 1971) that the numbers of hybrid plants and the 'number of species

involved seems to be exceptional', so much so that in some genera, e.g. *Senecio pro parte* and *Euphrasia*, hybrids are more frequently encountered than species. This is probably once again a measure of the large amount of open ground and high proportion of weedy species in the Orkneys. There are many genera in the British Isles where hybridization has occurred between native and alien species, e.g. *Heracleum*, *Calystegia*, *Linaria*, *Senecio*, *Tragopogon*, *Endymion*, *Juncus* and *Spartina*, besides others where it is also widespread among native species, and, if in these genera species have evolved allopatrically without the formation of sterility barriers, this is not surprising.

But none of these situations seems to resemble that concerning the Lancashire *Juncus* hybrids, and indeed the only apparently close parallel I can find is that described in *Equisetum* subgenus *Equisetum* by Page (1973). There are four hybrid combinations in this subgenus in the British Isles, one of which (*E. arvense* × *E. fluviatile*) is widespread. The other three are all confined in the British Isles to the Hebrides (where *E. arvense* × *E. fluviatile* also occurs): *E. arvense* × *E. palustre* occurs on the Isle of Skye and is not known elsewhere; *E. palustre* × *E. telmateia* occurs on Skye and in two Mediterranean localities (Gerona, Spain and Alpes Maritimes, France); and *E. fluviatile* × *E. palustre* occurs on the Isle of Harris and is again not known elsewhere. Page considers that all the hybrids have arisen independently in the Hebrides, and suggests that the damp, oceanic climate and the exposure of bare mud by digging of ditches (both of which would favour the growth of prothalli) have been instrumental in their formation.

In *Juncus* there is a good range of factors tending to prevent hybridization. Besides the slightly different geographical distributions the ecological preferences of all the species differ, although *J. balticus*, *J. effusus* and *J. inflexus* are all quite common in coastal dune-slack communities, in which the hybrids occur. There are also differences in the flowering time, although these are not absolute, and in chromosome number. There is evidently a fairly strong interspecific incompatibility system as well, for no artificial hybrids have been produced; foreign pollen germinates successfully but the pollen tubes cease growth before they reach the ovules. It is very difficult to imagine special features of the Lancashire coastal climate which might affect hybridization potential. There are perhaps four suggestions that one might make in trying to throw some light on the situation:

(a) The chromosome numbers of the five Lancashire hybrids, each indicating non-reduction in the parent other than *J. balticus*, are remarkable. But if this is other than a coincidence one still needs to explain the cause of non-reduction. *Juncus* pollen is dispersed in

tetrads, so that non-reduced pollen (diads) should be easily recognized. None has been seen in any species, although it is possible that non-reduction takes place on the female side, when *J. balticus* would have been the male parent of the hybrids.

(b) The Lancashire *J. balticus*, discovered in 1913, is 300 km removed from the next nearest colony (in eastern Scotland), and its origin is obscure. No differences in morphology, anatomy, chromosome number or compatibility with other species between Lancashire, Scottish and Scandinavian material of *J. balticus* have been detected, but the possibility remains that physiological differences do exist which have contributed to the formation of hybrids in Lancashire. Although there is no evidence that *J. balticus* was ever really common even locally in Lancashire, one colony is known to have been eradicated within the last 30 years (Stace, 1972), and it is thus possible that a distinctive Lancashire strain of the species has become extinct. It is quite conceivable that the Lancashire *J. balticus* has a very distant origin, for in recent years two other species of *Juncus* have become well established in the British Isles far from their native areas of distribution: *J. subulatus* from southern Europe, in the Bristol Channel (Willis & Davies, 1960), and *J. planifolius* from Australasia and South America, in W. Galway, Eire (Scannell, 1973).

(c) It is possible that the scarcity of hybrids is due to the lack of conditions suitable for hybrid establishment, but that such conditions are or were in some way provided on the Lancashire coast. Seedling establishment in subgenus *Genuini* is almost certainly dependent upon open conditions (Lazenby, 1955), and is then often very successful. In closed vegetation the plants probably increase solely by vegetative spread, and all the three species considered here can be strongly invasive. Of the five Lancashire hybrid colonies four are (or were) of considerable size and occur among dense dune-slack vegetation, into which they are spreading, but the fifth was only about 6 in. in diameter when it was discovered in 1966 in bare sand in the damp hollow of a sand dune. It would be expected, however, that many other areas in the band of overlap between the three species would offer similar opportunities for seedling establishment.

(d) There remains the possibility that the intensive field-work carried out by many botanists in Lancashire has led to the discovery of all the hybrid sites, whereas those elsewhere remain undetected. I do not consider this very likely, as there are many diligent and experienced Scottish and Scandinavian botanists who are very active field-workers, and German botanists have been aware of the possibility of hybrids involving *J. balticus* since the last century. *J. balticus* × *J. effusus* resembles and could be mistaken for *J. balticus* × *J. filiformis*, which

is common around the Baltic Sea coasts, but *J. balticus* × *J. inflexus* is a very distinctive plant less likely to have been overlooked.

One is therefore forced to the conclusion that no single known factor is implicated in the uneven and unexpected distribution of these *Juncus* hybrids. It is more likely that an interaction of a variety of factors is responsible for the present situation, and probably the balance is quite fine. In such cases it is usually impossible to predict the abundance of hybrids, even when experiments have provided a good deal of basic information, and it is surely likely that the *Juncus* example can be paralleled in many other groups. For this reason the continued intensive and extensive observation and recording by field-workers, coupled with experimentation by biosystematists, is essential. It is certain that close co-operation by amateur and professional plant taxonomists, so long a notable feature of the Botanical Society of the British Isles, will continue to be as fruitful as ever.

ACKNOWLEDGMENTS

I am grateful to Mr J. W. Grimes for much assistance in the investigations of hybridization in *Juncus*, and to the Science Research Council for providing a Research Grant.

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TAXONOMIC PROBLEMS IN THE FERN GENUS *POLYSTICHUM* CAUSED BY HYBRIDIZATION

G. Vida and T. Reichstein

ABSTRACT

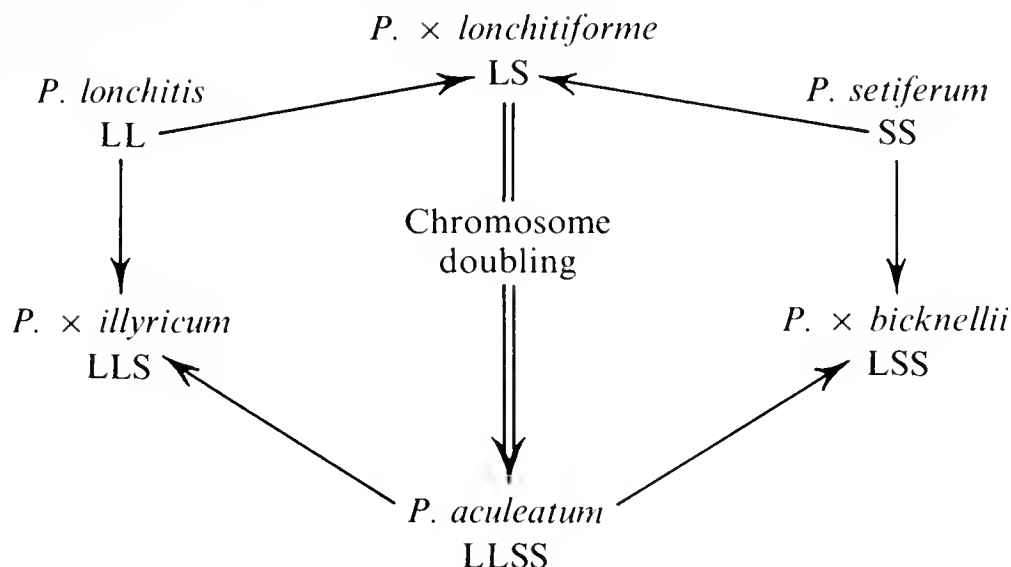
The genus *Polystichum* in Europe consists of two diploid species, *P. lonchitis* (LL) and *P. setiferum* (SS). A third allotetraploid species, *P. aculeatum* (LLSS) has long been formed between these diploids. The meiotic division, spore fertility and the progenies of the triploid $P. \times$ *illyricum* (LLS) were studied in order to demonstrate the degree of genetic isolation between *P. lonchitis* and *P. aculeatum*.

$P. \times$ *illyricum* exhibits at meiosis c. 41 bivalents and c. 41 univalents. Difficulties with the distribution of the univalents cause a high degree of spore abortion. A limited number of progeny, however, could be obtained by dense spore sowings. These plants were triploid or hexaploid (autoallohexaploid: LLLLSS). Analyses of meiosis and spore-formation in the triploid F_1 demonstrate the probable way of origin of the F_2 plants. The types of spore-formation in these triploid hybrids are discussed in connection with the possibility of gene exchange among the allotetraploid and its two diploid progenitors via triploid hybrids.

INTRODUCTION

The genus *Polystichum* in Europe is represented by two diploid and two tetraploid species as follows: *P. lonchitis* (L.) Roth, $2x$; *P. setiferum* (Forskål) Woynar, $2x$; *P. aculeatum* (L.) Roth, $4x$; *P. braunii* (Spenner) Fée, $4x$ ($x = 41$).

The first three are native to the British Isles. Hybrids in every combination have already been found (Meyer, 1960; Sleep & Reichstein, 1967; Vida, 1966) and synthesized (Sleep, 1966). According to the results of genome-analysis of these species (Manton, 1950; Manton & Reichstein, 1961; Sleep, 1966; Vida, 1966, 1972) the origin of the tetraploid *P. aculeatum* could be explained by the following scheme:



L = *P. lonchitis* genome (41 chromosomes)

S = *P. setiferum* genome (41 chromosomes)

P. x illyricum (Borbás) Hahne and *P. x bicknellii* (Christ) Hahne, both triploid hybrids, have been reported in many places where *P. aculeatum* grows together with *P. lonchitis* or *P. setiferum* (also in the British Isles: see Sleep, 1971; Sleep & Synnott, 1972). They can be regarded as back-crosses to one of the two diploid progenitors. At meiosis, therefore, they usually form bivalents between the chromosomes of the similar genomes (41 bivalents), while the remaining third genome is represented by unpaired chromosomes (41 univalents).

Morphologically (as well as ecologically) the two diploid species *P. lonchitis* and *P. setiferum* are very easy to distinguish. The alpine-boreal *P. lonchitis* has persistent, coriaceous, linear-lanceolate fronds with undivided pinnae. The chiefly Mediterranean *P. setiferum*, on the other hand, develops soft, sometimes not persistent, lanceolate fronds with clearly divided pinnae. Keeping in mind the above-illustrated origin of the tetraploid *P. aculeatum*, it is not surprising that this species is intermediate between its two diploid progenitors in almost every respect. This fact is reflected in some earlier taxonomic treatments of the group, giving subspecific rank to *P. setiferum* under *P. aculeatum*. Nevertheless, *P. lonchitis*, *P. aculeatum* and *P. setiferum* are distinct species which are not too difficult to identify provided the plant is not juvenile or stunted. The triploid hybrids, however, make this morphological distinctiveness almost completely continuous, since the range of variation of each taxon (incl. hybrids) overlaps to a large extent (Fig. 1).

The taxonomic difficulty is further increased by an interesting observation, namely, that at some places, where two *Polystichum* species (*P. lonchitis* and *aculeatum* or *P. setiferum* and *aculeatum*) have been growing together, presumably for many generations, there is an increased morphological similarity between the two cytologically different

species, which could also be expressed in numerical terms (Vida ined.). There are two alternative explanations for this phenomenon. One can argue that the morphological difference between two *Polystichum* species is a product of the very complex natural selection acting differently under dissimilar ecological conditions of these species. Accordingly, natural selection in the ecologically intermediate mixed populations favours genotypes approaching an intermediate morphology in both species. The other alternative possibility would be genetic introgression via hybridization and back-crosses, which is much more effective in achieving rapid genetic alterations, provided there is no strong reproductive barrier between the species concerned.

In order to test this second hypothesis we started to study the meiosis, spore formation, fertility and progenies of the two triploid hybrids (*P. × illyricum* and *P. × bicknellii*).

MATERIALS AND METHODS

(a) Source of the wild hybrids

Wild triploid hybrids were cultivated in Basel or Budapest of the following origin:

P. × illyricum

- TR-255 Switzerland, Kanton Schwyz, Schärsack, SE from Hagenegg, Mythen. Limestone, c. 1390 m. leg. TR. 27 July 1960. Cultivated in Basel (TR).
- TR-1767 Switzerland, Herrenrüti near Engelberg, leg. Dr W. Gätzi 1959. Cultivated in Basel (TR).
- TR-1768 Switzerland, Untertrübsee near Engelberg. Along the way to the Gentialp, leg. Dr W. Gätzi 1959. Cultivated in Basel (TR).
- GV-Pol. 8 Poland, Tatry: Giewont: limestone scree under *Picea* forest. Altitude 1400 m, leg. GV. 14 September 1962. Cultivated in Budapest (GV).

P. × bicknellii

- GV-Pol. 1a Hungary: Mecsek-Hills: Szuado Valley near Orfü, leg. GV. August 1961. Cultivated in Budapest (GV).
- GV-Pos. 2b Hungary: Bakony Hills: Tóth-árok Valley near Fenyőfő, leg. GV. August 1961. Cultivated in Budapest (GV).

(b) Cytology

Cytological investigations were carried out using the standard carmine squash method (Manton, 1950) for meiosis and sporangial development. Root trips were previously treated with colchicine (0.1 per cent for 3–5 h at 4 °C) followed by fixation in acetic–alcohol (3:1) and 5 h softening in a snail enzyme solution according to Roy & Manton (1965).

(c) Progeny yield

In order to avoid foreign spores in testing spore viability of the triploid hybrids, great care was taken to preserve the purity of spores and cultures. In Basel fronds with ripe spores (TR-1767, 1768, 2051) were collected from plants grown in the experimental garden, washed under running tap water and pressed to release the spores between two sheets of clean white paper. The spores were sown on a mineral solution solidified with 1 per cent agar and the prothalli when c. 1.5 mm long transplanted on sterilized soil in pots covered with transparent plastic cups.

In Budapest the experiments started much later, taking into account the previous results at Basel. Pots with large hybrid plants (GV-Pol. 8, Pol. 1 *a*, Pos. 2 *b*) have been kept separately in a greenhouse where there was no other *Polystichum* around. In spring as the new fronds started to unroll, they were covered with a paper bag, firmly sealed at the petiole. We fixed the bag in a position to allow the frond to develop inside the bag. One side of the paper bag was replaced by cellophane in order to make photosynthesis (and observations) possible. When the spores were ripe, the whole frond with the bag was cut and the sowing was subsequently made on agar just as in Basel.

RESULTS

(a) Cytology of the wild hybrids

The natural hybrids *P. × illyricum* (TR-255, 1767, 1768; GV-Pol. 8) and *P. × bicknellii* (GV-Pol. 1 *a*, Pos. 2 *b*) were all studied cytologically. Each one was found to be triploid with $2n = 123$ and $n = c. 41_{II} + 41_I$ at meiosis. Representative stages of the meiosis and spore formation are illustrated with *P. × illyricum* in Figs. 2–7 (Plate I). Large numbers of univalents disturb the meiotic division from the anaphase I onwards. These chromosomes seem to hesitate at metaphase I in the equatorial plate and either move to one of the poles at random or divide by distributing chromatids to the opposite poles. In this latter case the second anaphase exhibits further irregularities, because these chroma-

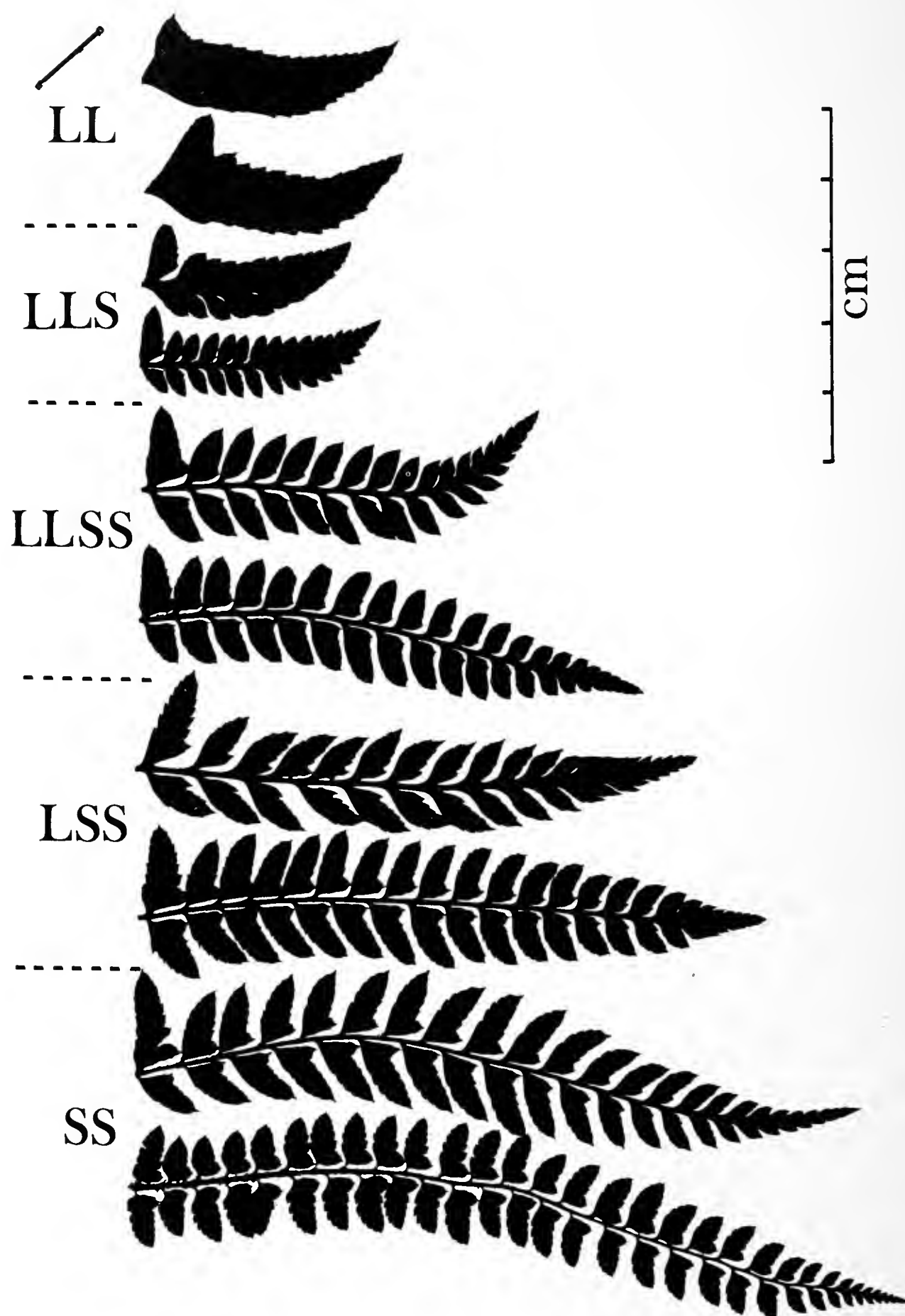


Fig. 1. Pinnae of *Polystichum* taxa taken from the middle of the frond. Genomic symbols: LL = *P. lonchitis*; LLS = *P. × illyricum*; LLSS = *P. aculeatum*; LSS = *P. × bicknellii*; SS = *P. setiferum*. Each taxon is illustrated by two extreme forms to show the overlapping characters.

Table 1

Culture	Data of sowing	Spore germination	Number of prothalli	Number of sporophytes	Ploidy (2n)				
					2x	3x	4x	6x	Unknown
<i>P. × illyricum</i>									
TR-1767	Basel 11.ix.1966	Numerous prothalli	Not estimated; dense culture	4	—	—	—	4	—
1768	Basel 11.ix.1966	Numerous prothalli	Not estimated; dense culture	3	—	—	—	1	2*
255B	Basel 19.viii.1967	Numerous prothalli	Not estimated; dense culture	9	1†	4	1†	—	2
GV-Pol. 8	Budapest 13.ix.1974	0.6%	10	(Expected later only)	—	—	—	—	—
<i>P. × bicknellii</i>									
GV-Pol. 1 a	Budapest 25.vii.1974	1.6%	c. 35,000	(Expected later only)	—	—	—	—	—
GV-Pos. 2 b	Budapest 25.vii.1974	1.9%	c. 30,000	(Expected later only)	—	—	—	—	—

* Poorly growing plants which died before a count was made.

† The diploid and tetraploid plants were probably contaminants of nearby *Polystichum setiferum* and *aculeatum* cultures.

tids cannot split again. In any case, the resulting tetrad consists of four nuclei (sometimes also a few micronuclei) with unbalanced chromosome sets, which causes an early abortion of the spores (Fig. 7).

In some sporangia, however, sporadic diad formation was also observed among the tetrads (Figs. 5, 6). These are of great importance, for potentially they can develop into viable spores, provided that all the 41 univalents behaved uniformly prior to diad formation.

(b) Fertility and progeny

Dense spore sowings were made from each hybrid plant with the results given in Table 1.

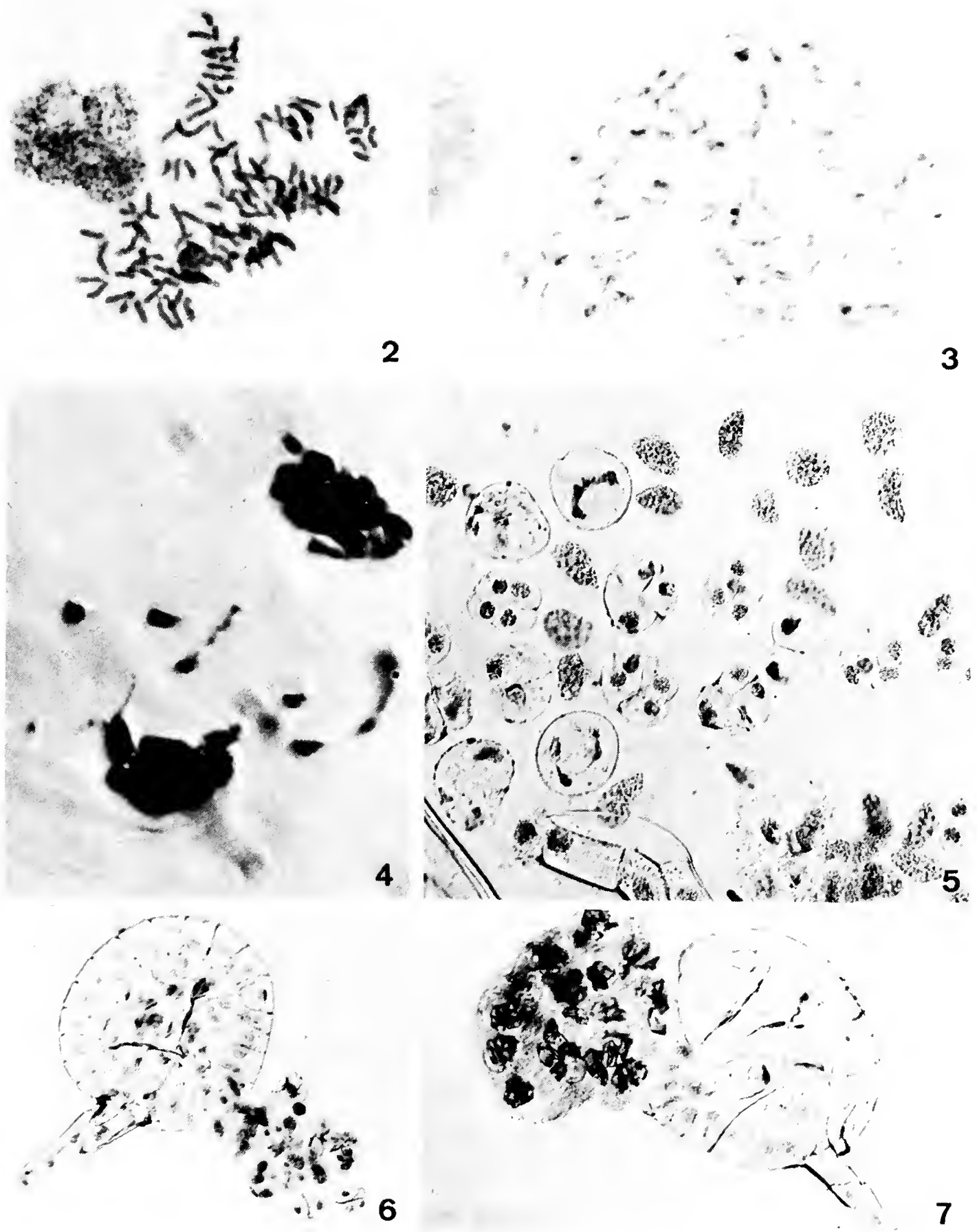
It is rather surprising that each plant produced an unexpectedly large number of prothalli. These prothalli, however, developed very slowly and many of them showed abnormal morphology. So far, only the earlier spore sowings (Basel) were able to develop a few sporophytes, but these were very interesting. Two cultures of *P. × illyricum* (TR-1767 and 1768) produced only 6x plants (Figs. 9, 13, 14) growing very slowly but eventually giving rise to a more or less fertile autoallohexaploid (genome symbol: LLLLSS) with morphology of *P. × illyricum*. On the other hand, TR-255B gave mainly triploids (Figs. 8, 10–12) showing vigorous growth but a striking variation in morphology when mature, two plants imitating *P. aculeatum* (except for bad spores), while two others looked like normal big *P. × illyricum*. The meiosis in these triploid progenies seems to be similar to the wild mother plant (presumably F_1), but their fertility appears to be slightly increased, which is illustrated by the greater number of healthy spores in the developing sporangia (Figs. 11, 14). Here again, diad formation was observed in many sporangia.

The result of *P. × bicknellii* progeny (GV-Pol. 1a, Pos. 2b) at this stage merely confirms the fact shown by *P. × illyricum* that triploid hybrids in this combination are also able to produce F_2 progenies. Nothing is known, however, about the chromosome number of the prothalli, although they show markedly different cell sizes, which could be connected with different ploidy levels.

DISCUSSION

The ability of interspecific triploid hybrids to produce functioning gametophytes (and consequently sporophytes) has not been seriously considered in ferns.* This is not infrequent, however, in flowering

* Intraspecific triploid hybrids of *Osmunda regalis* have been studied in this respect by Manton (1950).



Figs. 2-7 (Plate I). Cytology of wild *P. x illyricum* (TR-1767 and 1768 a).

Fig. 2. Root tip mitosis with $2n = 123$ chromosomes (TR-1768 a). $\times 1000$.

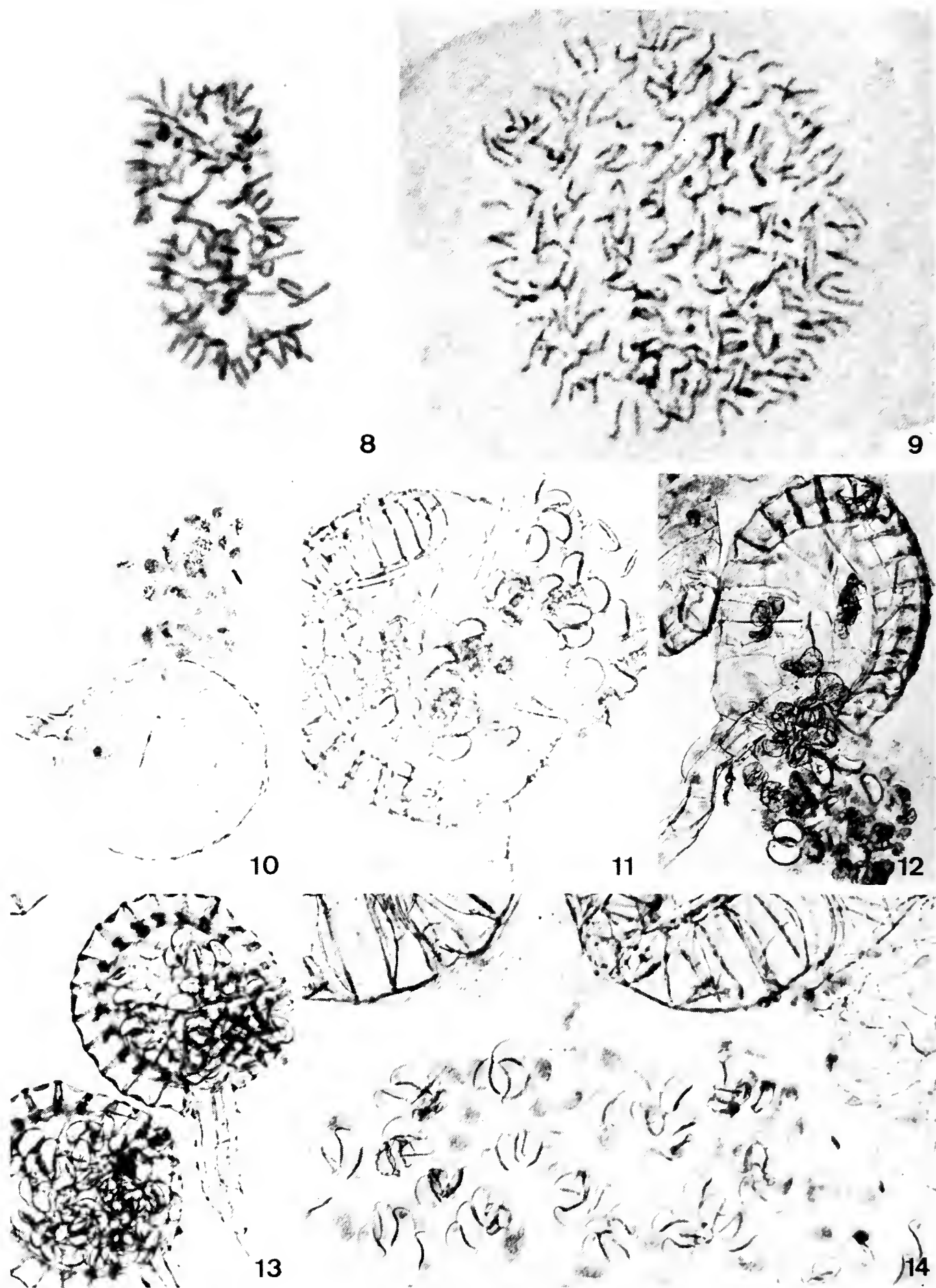
Fig. 3. Meiosis (dikinesis) showing 41 bivalents and 41 univalents (TR-1768 a). $\times 1000$.

Fig. 4. Meiotic telophase I (TR-1767) showing lagging univalents partly forming micronuclei between the opposite poles. $\times 1000$.

Fig. 5. The results of meiosis in TR-1767. Tetrads, diads and intermediate forms. $\times 600$.

Fig. 6. Content of a young sporangium after meiosis (TR-1768 a) with some diads. $\times 300$.

Fig. 7. Entirely aborted spores in a sporangium of TR-1768 a. $\times 300$.



Figs. 8–14 (Plate II). Cytology of the progenies of wild *P. x illyricum*.

Fig. 8. Root tip mitosis in a triploid progeny (TR-255B-pr.4). $2n = c. 123$. $\times 1000$.

Fig. 9. Root tip mitosis in a hexaploid progeny (TR-1767-pr.1). $2n = 246$. $\times 1000$.

Fig. 10. Spore mother cells at the first meiotic metaphase in a sporangium of a triploid progeny (TR-255B-pr.2). $\times 300$.

Fig. 11. 'Good looking' and aborted spores in a sporangium of the same plant (as Fig. 10). $\times 300$.

Fig. 12. Aborted tetrad-spores and apparently viable diad-spores in a triploid progeny (TR-255B-pr.6). $\times 300$.

Fig. 13. Normal, viable spores in a hexaploid progeny (TR-255B-pr.7). $\times 300$.

Fig. 14. Viable tetrad-spores of a hexaploid progeny (TR-1767-pr.3). $\times 300$.

plants, where in some cases it may give rise to back-crosses as well. This can cause unilateral introgression from the diploid to the tetraploid species (e.g. in *Dactylis* – Zohary & Nur, 1959).

The degree of fertility of triploid flowering plants is usually markedly different on the male and female sites. Sometimes unidirectional movement of the univalent chromosomes at the female meiosis includes all the chromosomes of the odd genome(s) into the functioning megaspore, thus giving rise to a viable embryo-sac (cf. Lewis & John, 1963, p. 337). At the same time the distribution of univalents in the pollen mother cells is much more random, resulting in only a low percentage of germinable pollen grains.

Basically the latter is true for the isosporous ferns too. Here the probability of a balanced chromosome set after the meiotic divisions is further decreased by the high base number ($x = 41$ in *Polystichum*). Supposing a random distribution of the 41 univalents, the occurrence of the extreme situation 0 and 41 at the opposite poles is rather unlikely ($1/2^{41}$), even if we consider the large number of trials (c. 10^5 – 10^7 per frond). We cannot be sure, however, that the univalent distribution is really a random process. It is also disputable that only spores with complete genomes are viable. Furthermore, the observed occurrence of diads instead of tetrads in some spore formation tells us that this distributional difficulty can probably be overcome by suppressing the meiotic process after the first division. In any case, the meiosis determines the fate and genetic character of the resulting spores.

Theoretically, a triploid fern hybrid (HHN) with two homologous (HH) genomes and a single unrelated non-homologous (N) genome can result in the following types of spore formation:

Type 1

Meiosis I. Equal distribution of chromosomes of the even genomes; unequal distribution and often 'micro-nuclear' separation of the univalents (odd genome).

Meiosis II. Separation of chromatids.

Result: 4 abortive spores + a few very small shrunken extra-spores from the 'micronuclei'.

Sporophyte: none.

Type 2

Meiosis I. Equal distribution of chromosomes (paired genome); equal distribution of chromatids (univalents).

Meiosis II. Blocked.

Result: 2 large viable spores with unreduced ($3x$) chromosome sets.

Sporophyte: via selfing, $6x$; via apogamy, $3x$ (as the F_1 plant).

Type 3

Meiosis I. As in Type 2.

Meiosis II. Equal distribution of chromatids of the even genome; unequal distribution of chromatids of the odd genome.

Result: same as in Type 1.

Sporophyte: none.

Type 4

Meiosis I. As in Type 2.

Meiosis II. Equal distribution of chromatids of the even genome; inclusion of all the chromatids of the odd genome into one of the opposite poles.

Result: larger diploid and smaller haploid spores genetically equivalent to the two parental species of the F_1 hybrid.

Sporophyte: via selfing, $2x$ and $4x$ parental species (P_1 , P_2); via hybridization, $3x$ hybrid as the F_1 .

Type 5

Meiosis I and II. Same as in Type 4, but instead of inclusion of the odd genome into one of the opposite poles, it remains alone and forms an extra nucleus between them.

Result: 5–6 small spores, each consisting of a haploid genome of either the 'odd' or the 'even' genomes.

Sporophyte: diploid species, one identical with the $2x$ parent of the F_1 , and the other one identical with a diploid species apparently not involved directly in the F_1 (being the other $2x$ progenitor to the tetraploid parent).

Type 6.

Chromosomes are doubled prior to meiosis, consequently there is a normal meiosis (as a $6x$ plant).

Result: 4 large triploid spores.

Sporophyte: same as in Type 2.

Out of these theoretical alternatives only Types 1, 2 and 3 were observed in meiosis of both *P. × illyricum* and *P. × bicknellii*. From these only Type 2 can yield progeny. Unfortunately we do not know whether they formed sporophytes sexually or asexually. The almost equal number of $3x$ and $6x$ F_2 sporophytes supports the assumption that both sexual and apogamic reproduction can occur in the case of a triploid gametophyte. The fact that the frequency of Type 2 spore formation (diads) has been increased in F_2 plants can be explained by its high selective advantage. After many generations this could probably lead to an established special form of apogamic reproduction.

Although Types 4 and 5 have not been unequivocally observed, their possibility cannot be ruled out. Intermediates between Types 3 and 4 have actually been seen in some cases. One of the reasons for setting up a new, large-scale experiment in Budapest was to demonstrate the occurrence of these types in *Polystichum* hybrids. If they really exist,

they could explain the putative introgression between *Polystichum aculeatum* and the related diploid species. On the other hand backcrosses of a hexaploid *P.*×*illyricum* or *P.*×*bicknellii* would almost surely be completely sterile because of the further difficulties with multivalent chromosomes, and introgression in this way is hardly possible.

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APPENDIX I

Ten special demonstrations were mounted for the Conference. Summaries or short papers based on four of these demonstrations are given below. The others, not separately discussed here, were as follows.

B.S.B.I. and Council for Nature: 'Save these Flowers' – a conservation exhibit.

*Mr B. Mathew and Miss C. A. Brighton: Cytotaxonomy of *Crocus*.

Mr and Mrs D. Parish: Colour photographs of flowers of Europe.

*Dr C. A. Stace: Hybrids in *Juncus* section *Genuini*.

Dr S. M. Walters: Index to the rare endemic plants of Europe.

Dr S. M. Walters and others: Problems of local floristic conservation.

The two exhibits marked * illustrated papers given to the Conference, and therefore printed in the main text of this volume.

RANGE EXTENSIONS IN THE HYDROCHARITACEAE

C. D. K. Cook

Of the 12 fresh-water genera of the Hydrocharitaceae only 2 (*Maidenia* and *Nechamandra* – both possibly congeneric with *Vallisneria*) show any inclination to 'stay at home'. It is difficult to say why this family is particularly well-equipped for extending its range. Many species are attractive or interesting aquarium plants and many introductions are a direct result of the aquarium trade. However, some species such as *Blyxa japonica* and *Ottelia alismoides* are ricefield weeds and were probably introduced with imported rice seed. In their native ranges many Hydrocharitaceae are found in eutrophic or brackish conditions, and may therefore be pre-adapted for various kinds of chemical pollution. Another factor probably encouraging their establishment in Europe is thermal pollution, and it is interesting that most of the recent introductions are plants of warmer regions.

The following is a list of genera and recent range extensions. The pondweed genera (*Egeria*, *Elodea*, *Hydrilla* and *Lagarosiphon*) are dealt with at the end.

Blyxa: c. 10 species, native in the warmer regions of Asia. *B. aubertii* has become naturalized in N. America, and *B. japonica* has become naturalized in Europe (northern Italy).

Hydrocharis: 3–6 species, native in the Old World. *H. morsus-ranae*, native in Europe, has become established in N. America.

Limnobium: c. 3 species, native in the warmer parts of S. America. *L. laevigatum* has become established in S. Europe and Java.

Maidenia: 1 species, *M. rubra*, native in N.W. Australia. It is a poorly studied plant and is possibly congeneric with *Vallisneria*.

Nechamandra: 1 species, *N. alternifolia*, native in India and S.E. Asia. It is possibly congeneric with *Vallisneria* although recent workers have combined it with *Lagarosiphon* and *Hydrilla*.

Ottelia: c. 40 species, native in the warmer parts of the world, 1 species in Brazil and the rest in the Old World with centres of speciation in central Africa and southern China. This genus is much in need of revision. *O. alismoides* [*O. japonica*] is naturalized in Europe (northern Italy).

Stratiotes: 1 species, *S. aloides*, native in Europe and northern Asia. It is apparently extending its range in Europe and has been reported as introduced in N. America.

Vallisneria: 6 to 10 or more species, cosmopolitan but absent from cold regions. This genus is much in need of revision. *V. spiralis* is extending its range in Europe; this and other species are apparently extending their ranges in many other parts of the world.

The pondweeds (*Egeria*, *Elodea*, *Hydrilla* and *Lagarosiphon*) in the vegetative phase are rather alike. For absolute certainty in determination flowers are necessary. The following is an attempt at a key, based on vegetative characters,

to the pondweeds introduced into Europe. It is possible that additional species may exist in Europe. Flowering material should be collected and sent to a botanical centre, or reference should be made to the cited works of Obermeyer and St John.

- 1A Leaves spirally arranged (at least at base of stem)
- 2A Leaves stiffly recurved, usually densely packed, up to 2.5 cm long
Lagarosiphon major
- 2B Leaves flaccid, spreading, not densely packed, very rarely
more than 1.5 cm long *Lagarosiphon muscoides*
- 1B Leaves in whorls or opposite pairs
- 3A Leaves usually reflexed, flaccid, densely packed together,
usually exceeding 2 cm in length *Egeria densa*
- 3B Leaves spreading, not reflexed, flaccid, rarely densely
packed, rarely exceeding 2 cm in length
- 4A Leaves usually in whorls of more than 3 (often 6–8)
- 5A Teeth on margins of leaves distinctly visible to naked eye; whorls of
fewer than 8 leaves not frequent *Hydrilla verticillata*
- 5B Teeth on margins of leaves barely visible to naked eye; whorls of
fewer than 8 leaves very frequent
- 6A Teeth on margins of leaves just visible to naked eye; female
flowers with large showy petals *Egeria najas*
- 6B Teeth on margins of leaves not visible to naked eye; female
flowers without petals *Elodea nuttallii*
- 4B Leaves rarely in whorls of more than 3
- 7A Leaves elliptic to ovate-lanceolate, with rounded apex, rarely more
- 7B Leaves gradually tapering into a long, narrow, pointed tip, up to
2 cm or more long
- 8A Leaves in whorls of 2 to 6; middle part of leaf up to 2 mm wide;
leaf margins curving to a pointed tip; sepals of female
flowers rarely more than 2 mm long; styles forked at tip
Elodea nuttallii
- 8B Leaves opposite or in whorls of 3; middle part of leaf rarely more
than 1 mm wide; leaf margins straight at apex, gradually
tapering to a very fine pointed tip; sepals of female flowers
up to 3 mm or more long; styles deeply forked *Elodea ernstae*

Egeria: like *Elodea* but male spathe 2- to 4-flowered; female spathe split halfway down one side; petals showy, about 3 times larger than sepals; stamens 9(–10). Occasionally included within *Elodea*: see St John, H. Monograph of the genus *Egeria* Planchon. *Darwiniana* 12: 293–307, 523 (1961).

2 species, native in warm temperate S. America. *E. densa* has become naturalized in Europe, Japan, Africa, N. and Central America, Australia and New Zealand. *E. najas* is sporadic in northern Europe. It is a popular aquarium plant but apparently does not persist in Europe.

Elodea [*Anacharis*]: c. 17 species in N. and S. (but not Central) America. Three species are found in Europe, but other species might be expected. Introduced plants of *Elodea* are nearly always female. St John, H. Monograph of the genus *Elodea*. I. The species found in the Great Plains, the Rocky Mountains, and

ERRATUM

Page 138 after 7A in key

remainder of sentence is missing; this should read:

than 1.5 cm long; plants usually robust *Elodea canadensis*

the Pacific States and Provinces of North America. *Res. Stud. Wash. State Univ.* 30: 19–44 (1964). II. The species found in the Andes and western South America. *Caldasia* 9: 95–113 (196n). III. The species found in northern and eastern South America. *Darwiniana* 12: 639–52 (1963). IV. The species of eastern and central North America, and Summary. *Rhodora* 67: 1–35, 155–80 (1965).

Elodea ernstae (often incorrectly determined as *E. callitrichoides*) is native in S. America and naturalized in S.E. England, France and perhaps elsewhere. It is very like *E. nuttallii* in the vegetative stage.

Elodea canadensis is native in N. America but has become established in Europe, Asia, Australia, New Zealand and Africa. It was introduced into the British Isles in 1836 and spread rapidly causing great alarm. Today it is widespread but has settled down and is no longer considered to be troublesome.

Elodea nuttallii [= *E. occidentalis*] is native in N. America but has become established in Holland, Belgium, ?France, northern Germany, northern Switzerland and ?British Isles. The so-called *E. nuttallii* from Esthwaite Water and western Galway is much smaller and more delicate than the *E. nuttallii* actively spreading in Continental Europe. Flowering material of the British plants is needed before one can be sure of their identity.*

Hydrilla: 1 species, *H. verticillata*, native in tropical and temperate Asia and northern Europe (Upper Dnieper, Lithuania, Latvia and northern Poland). It has not been found in W.C. or S. Europe but has become naturalized in S.E. U.S.A. It can be distinguished from *Elodea* and *Egeria* by the larger teeth on the leaf margin and the regularly high number of leaves (c. 8) in each whorl.

Lagarosiphon: c. 16 species, native in Africa and Malagasy: see Obermeyer, A. The African species of *Lagarosiphon*. *Bothalia* 8: 139–46 (1964). It can be distinguished from *Elodea*, *Egeria* and *Hydrilla* by the spirally arranged leaves. *L. major* is established in Europe and New Zealand. *L. muscoides* is sporadic in Europe. It is a popular aquarium plant but apparently does not persist in nature.

Editor's note

The exhibit by Professor Cook showed living material of a number of fresh-water aquatic plants of taxonomic interest to European botanists. In this short account the author has concentrated on the Hydrocharitaceae, species of which in recent years have significantly extended their range in parts of Europe.

Professor Cook's new book, *Water Plants of the World* (Junk, The Hague, Netherlands), the publication of which is expected as this Conference report goes to press, will undoubtedly make a very valuable contribution to the taxonomic and ecological understanding of the fresh-water flora of the world.

* Since this paper was given, Professor Cook has received good material of *E. nuttallii* collected near Oxford, by Mr R. Palmer.

IDENTIFICATION BY POLYCLAVE

R. J. Pankhurst and R. R. Aitchison

A method of identification by using punched cards (a polyclave) was demonstrated. This works by putting together cards in the hand for each character of the specimen, and eliminating any taxon which does not agree. At the end the position of the clear hole(s) in the pack of cards indicates which taxon (taxa) is the answer.

The method is more convenient than a conventional key because any characters can be used in any sequence. The novelty shown here is that the cards are derived and manufactured by computer. This means that such keys are easy to create and to revise, and cheap to produce. Keys were shown for the British microspecies of *Rubus* (400) and *Taraxacum* (133). The computer program (Pankhurst & Aitchison, 1975) and documentation are available on request (RJP). The *Rubus* polyclave and descriptions of how to use it are also available from RJP.

Reference

Pankhurst, R. J. & Aitchison, R. R. (1975). 'A computer program to construct polyclaves.' In *Proceedings of meeting on 'Automatic Identification of Biological Specimens'*, ed. R. J. Pankhurst. London: Academic Press.

MAPPING THE EUROPEAN VASCULAR PLANT FLORA

J. Suominen

(1) *Atlas Florae Europaeae* (AFE; vols. 1 and 2 published) consists of maps showing the European distribution of species and subspecies. Established introductions and extinctions are indicated by special symbols. Textual comments on the maps give important synonyms, notes on taxonomy and nomenclature and important new or omitted records (mainly complementing or correcting *Flora Europaea*) as well as references to total range maps. A map in vol. 1 (p. 11), which gives the numbers of species of Pteridophyta in the 50-km squares, reveals the differences in the richness of the flora, and also reflects variation in the intensity of floristic research.

(2) *Goal of AFE*. The atlas is independent of *Flora Europaea*, although it has close connections with that work, as it complements the distributional information given there. The basic aim is to proceed in systematic order and include all the taxa that can reasonably be mapped. This is a most fundamental point and distinguishes AFE from all the other European mapping projects undertaken so far, which either do not cover the whole of Europe or do not include all the European species. In view of the high standard of many of these atlases, the fact that all the European species will be included in taxonomical order seems to be the main reason and justification for the preparation and publication of AFE. It is hoped that the regrettable necessity of publishing many incomplete or even provisional maps may serve as a stimulus to further botanical research, both taxonomical and chorological.

(3) *Method of producing AFE*. Each European country is represented by one (sometimes more) member of the Committee for Mapping the Flora of Europe (CMFE). He, with assistant botanists, is responsible for collecting floristic data for the 50-km UTM grid squares in his country. These national data, usually entered in a section of the base map, are submitted to the secretariat of the CMFE in Helsinki. The secretariat uses the maps from the different countries to compile the final European maps and prepares the textual comments on the maps. The map and text drafts are then sent for checking to the Committee members and some specialists in taxonomy before they are printed.

The individual countries meet the cost of collecting their own records. The secretariat receives a yearly grant from the Finnish Ministry of Education to cover technical and material expenses. AFE is published by Societas Biologica Fennica Vanamo and distributed by Ticto Ltd., 5 Elton Road, Clevedon, Avon BS21 7RA.

(4) *Historical background of the CMFE and AFE*. Two important events in European botany preceded the launching of the scheme to map the distribution of the European vascular plant flora. These were the publication of the *Atlas of the British Flora* in 1962 and the completion of vol. 1 of *Flora Europaea* in 1964. The commencement of the mapping scheme was British as well. At the

Tenth International Botanical Congress in Edinburgh in 1964 Dr F. H. Perring presented a map showing the 50-km-square distribution of *Silene acaulis*. He then organized a network of European botanists to take part in a mapping experiment with ten species, the results of which were displayed at the Fourth Flora Europaea Symposium in Århus, Denmark, where the CMFE was founded in August 1965. The secretarial duties were offered to Helsinki and the secretariat was installed there in December 1965.

During the subsequent years further experiments were undertaken and a mapping team was organized to cover all the European countries. The results of these experiments and questions relating to mapping techniques and the organization of the scheme were discussed by the CMFE at meetings held in 1966 in Cracow, Poland, and in 1968 in Halle, DDR. By 1973, when a meeting took place in Varna, Bulgaria, the two first volumes of AFE had been published, and the main topic of the meeting was what steps should be taken to ensure that the following volumes of AFE were completed at a reasonably rapid rate.

(5) *The production of AFE – present situation and future prospects.* The use of a network of national representatives has many valuable advantages, making it possible to utilize local sources of information and the most recent records, to avoid errors in the literature and those caused by misleading place-names, and to reach satisfactory decisions as to the native or introduced status of plants and extinctions. However, such a team is really effective only when each country is able to keep up with the others. Here lies the weak point of the mapping scheme. Occasional difficulties and other duties may prevent committee members from submitting data in time, and a delay in any single European country can easily hold up the entire mapping scheme and retard the publication of AFE. In view of the fact that only a small percentage of the European vascular plant species has so far been mapped in AFE, it is absolutely essential for the continuation of the mapping scheme and the completion of the atlas to find some means of working to a reasonable schedule.

SOME EUROPEAN GERANIUMS WITH ASIATIC CONNECTIONS

P. F. Yeo and H. Kiefer

The work in progress consists of (a) a biosystematic investigation into various groups of species within which there are known or suspected micro-evolutionary affinities, (b) an attempt to arrive at an improved classification of the genus, including the use of computer-generated groupings.

The exhibit showed two species-groups, (1) the *G. pratense* group, showing that various Central Asian and Himalayan forms can be considered as either falling within *G. pratense* or being closely related to it; (2) the *G. cinereum* group, consisting of a series of geographical vicariants extending from N.W. Africa through Spain, the Alps, Italy, the Balkans and eastern Turkey; specific separation of *G. argenteum* from the rest of the group appears questionable.

APPENDIX II

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